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Spore Morphology of the Hawaiian Genus Sadleria (Blechnaceae)

ROBERT M. LLOYD*,[1]

The Blechnaceae is a small family of terrestrial ferns which includes about eight genera. The family is characterized by fronds with elongate sori (discrete or forming coenosori) on a secondary vein which runs parallel to the midvein of the pinna. These sori are protected by introrse indusia which open toward the costae. Most of the genera of Blechnaceae have a circumtropical, Southern Hemisphere distribution.

The genus *Sadleria* Kaulf. is one of three fern genera endemic to the Hawaiian Islands. Nine species have been described in the genus, including *S. cyatheoides* Kaulf., *S. pallida* Hook. & Arn., *S. souleyetiana* (Gaud.) Moore, *S. squarrosa* (Gaud.) Moore, *S. polystichoides* (Brack.) Heller, *S. unisora* (Bak.) Robinson, *S. hillebrandii* Robinson, *S. fauriei* Copel., and *S. rigida* Copel. Past taxonomic treatments have recognized a variety of species. Hillebrand (1888) recognized four: *S. cyatheoides, S. pallida, S. souleyetiana*, and *S. squarrosa*, the last species with three varieties. Christensen (1925) recognized seven species, including in addition to the above *S. fauriei*, *S. rigida*, and *S. unisora*. Copeland (1947) and Stone (1967) mentioned that six or seven species exist in the genus. A modern treatment of the genus is lacking.

The species of *Sadleria* are found in a variety of ecological habitats, from bare lava flows to wet rain forests. The most common species, *S. cyatheoides*, is among the first invaders of new lava flows, but is found as well in nearly mature *Acacia-Metrosideros-Cibotium* forest. The remaining species are less common; *S. squarrosa*, for example, is restricted to wet, dark banks in upland rain forest.

Morphologically, the genus is much like *Blechnum*. However, in contrast to the usually non-arborescent rhizome and pinnatifid to pinnate fronds of most *Blechnum* species, the rhizome of *Sadleria* is erect and in most species arborescent and the fronds are bipinnatifid to bipinnate.

There is little available literature on spore morphology in *Sadleria*. Previous studies dealing only with spore size and shape include those by Skottsberg (1942), Selling (1946), Carlquist (1966), and Holbrook-Walker and Lloyd (1973). The following study was undertaken to document more fully spore morphology in this unusual genus, utilizing the scanning electron microscope, to see if this feature could provide insights into the taxonomic relationships of the species.

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*Department of Botany, Ohio University, Athens, OH 45701.

[1] Appreciation is expressed to the curators of the herbaria cited within for lending the specimens on which this study is based. I would also like to acknowledge Dr. Otto Degener for his helpful comments and for making available to me his specimens of the genus for study. This work was supported by NSF grant GB-36923.

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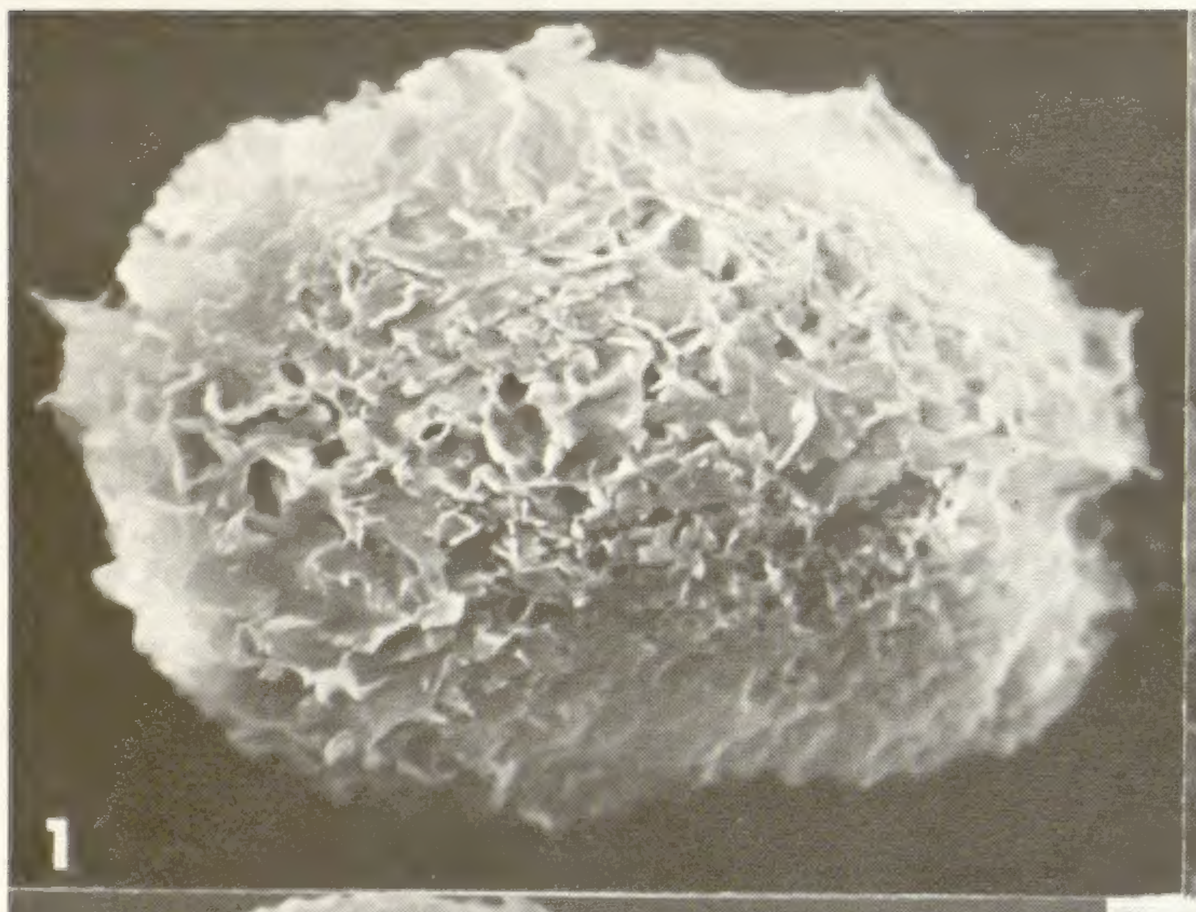
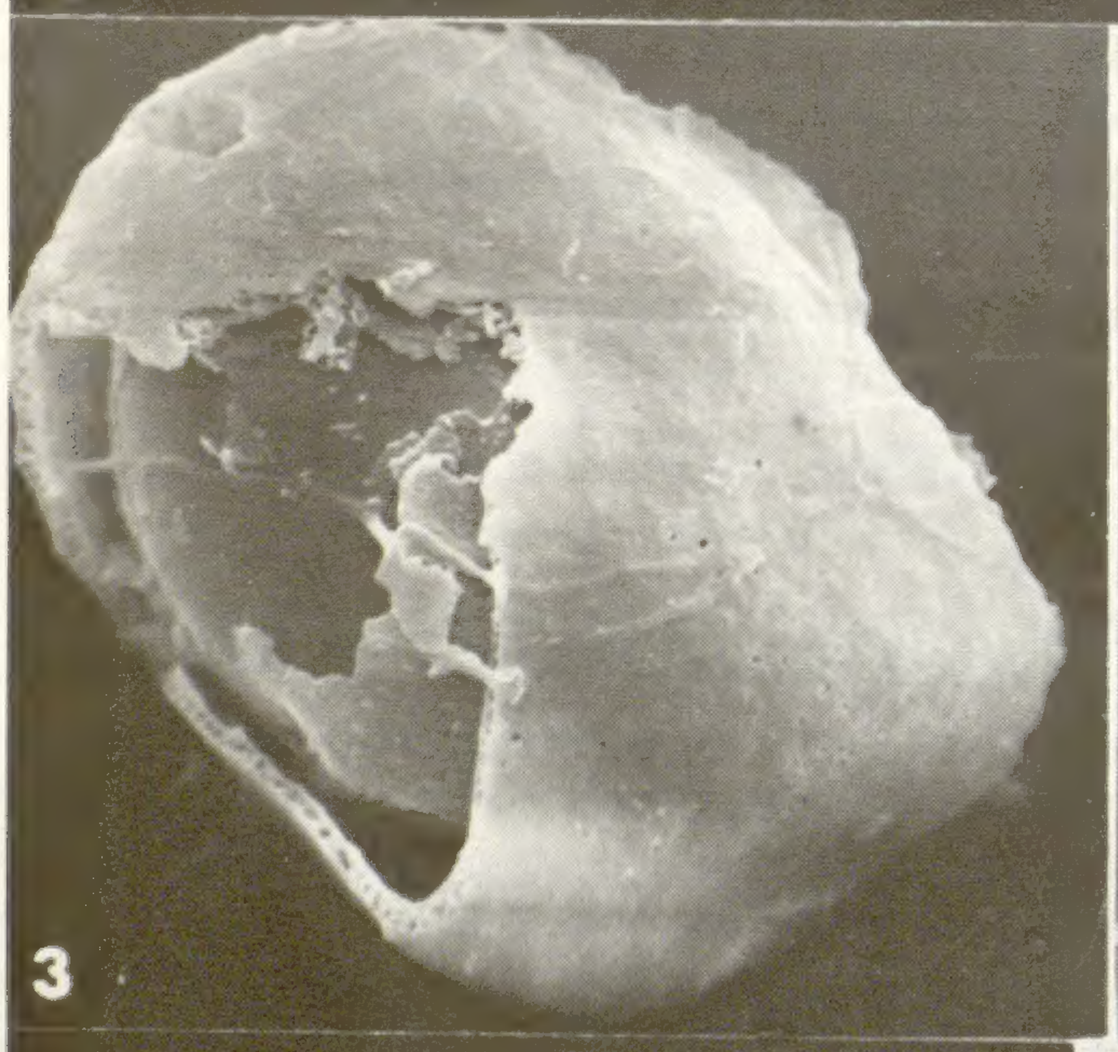
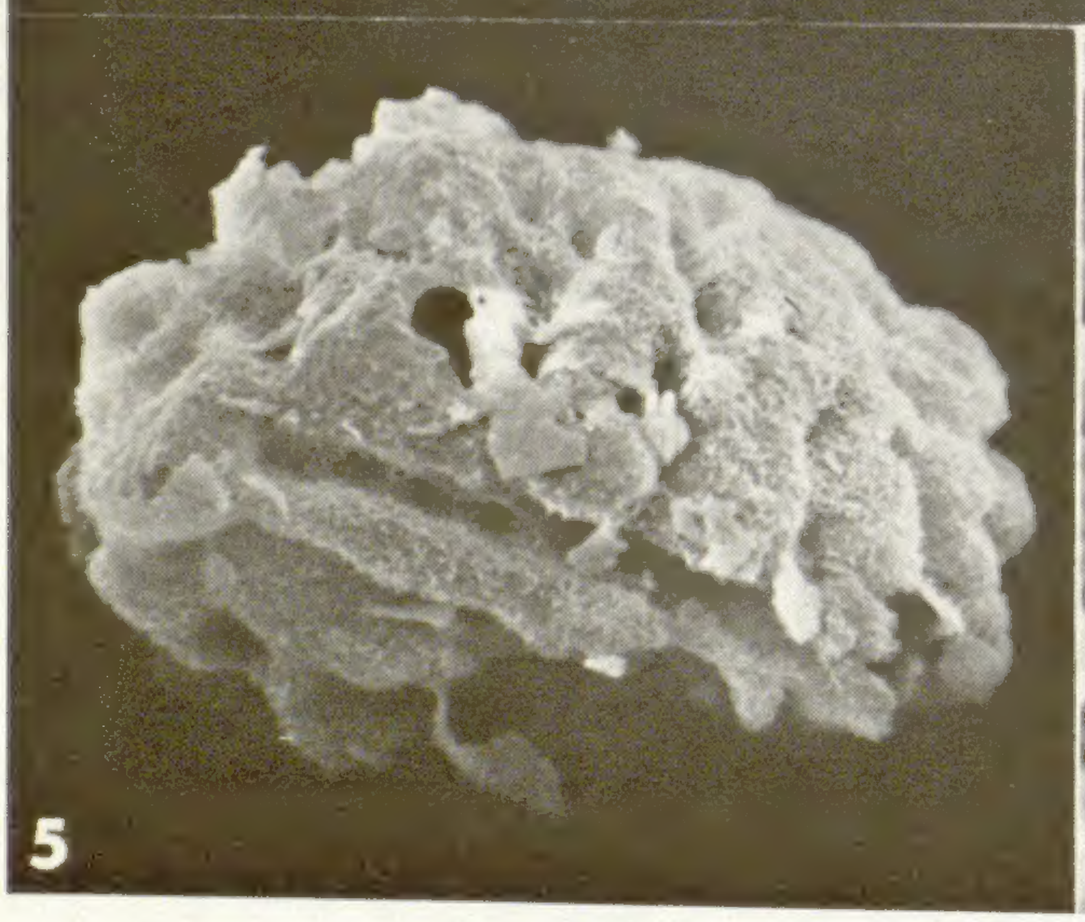
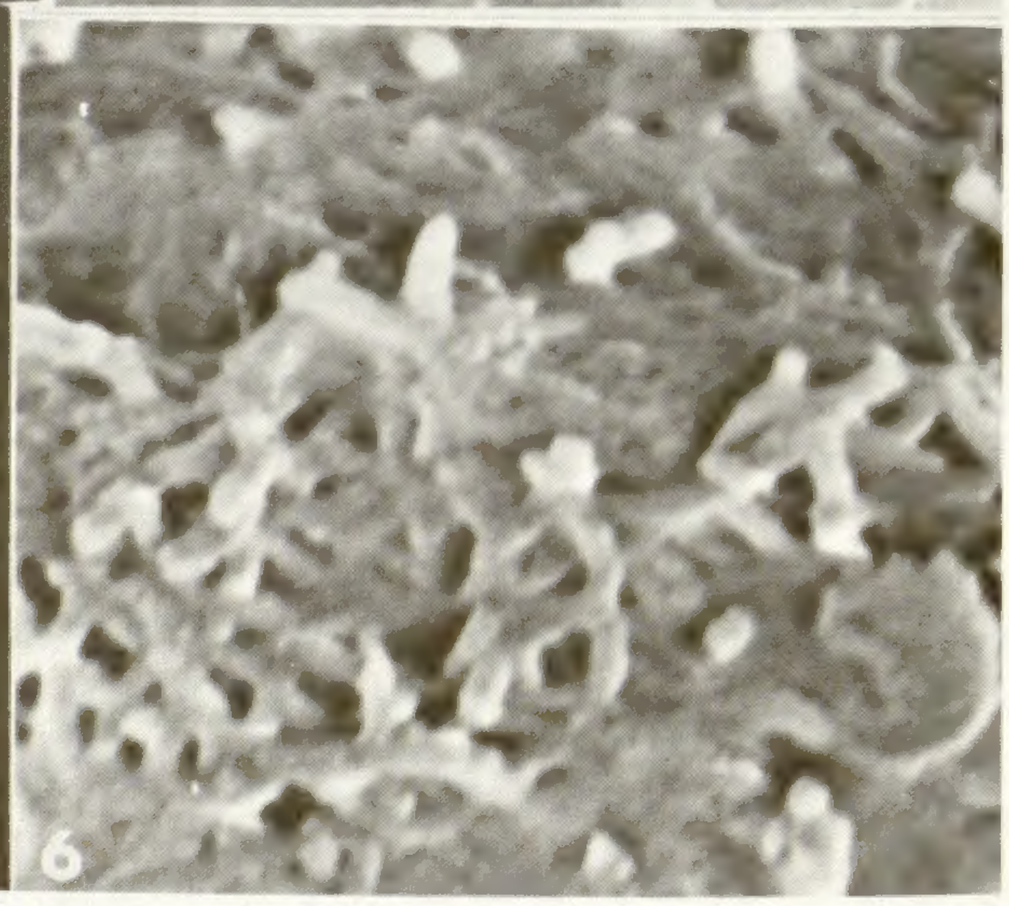








Sadleria spores. FIG. 1. *S. hillebrandii, St. John et al. 18447* (MICH), × 1200. FIG. 2. *S. hillebrandii*, surface view, *St. John et al. 18447* (MICH), × 3000. FIG. 3. *S. cyatheoides*, showing broken, multilayered perispore, *Degener 18502* (GH), × 1200. FIG. 4. *S. cyatheoides*, surface view, *Degener 18502* (GH), × 5000. FIG. 5. *S. souleyetiana, St. John 24727* (MICH), × 1100. FIG. 6. *S. souleyetiana*, surface view, *St. John 24727* (MICH), × 6000.

MATERIALS AND METHODS

Spores were obtained from herbarium specimens of most taxa of *Sadleria*. Untreated spores were mounted on specimen stubs with double-stick tape, coated with gold approximately 10 nm thick, and observed at 20 kv accelerating voltage with a Hitachi HHS-2R scanning electron microscope. Spore sizes were obtained from spores mounted in diaphane and observed with light microscopy. The voucher specimens are:

S. cyatheoides: Hawaii: *St. John & Catto 18423* (MICH). Lanai: *St. John & Eames 18752* (MICH). Maui: *Degener 18502* (GH). Oahu: *Copeland s. n.* (MICH), *Fosberg 13309* (MICH).

S. hillebrandii: Hawaii: *St. John et al. 18447* (MICH). Maui: *Bonsey s. n.* 13 Aug 1951 (MICH).

? S. cyatheoides × hillebrandii: Hawaii: *Degener 18494y* (GH).

S. pallida: Oahu: *Degener 10329* (MICH), *Fosberg 13665* (MICH).

S. souleyetiana: Maui: *St. John 24725, 24727* (MICH).

S. squarrosa: Lanai: *Munro 940* (NY). Molokai: *Crosby & Anderson 1696* (MICH). Oahu: *Grether & Wagner 3924* (US), *Wagner 5756* (MICH).

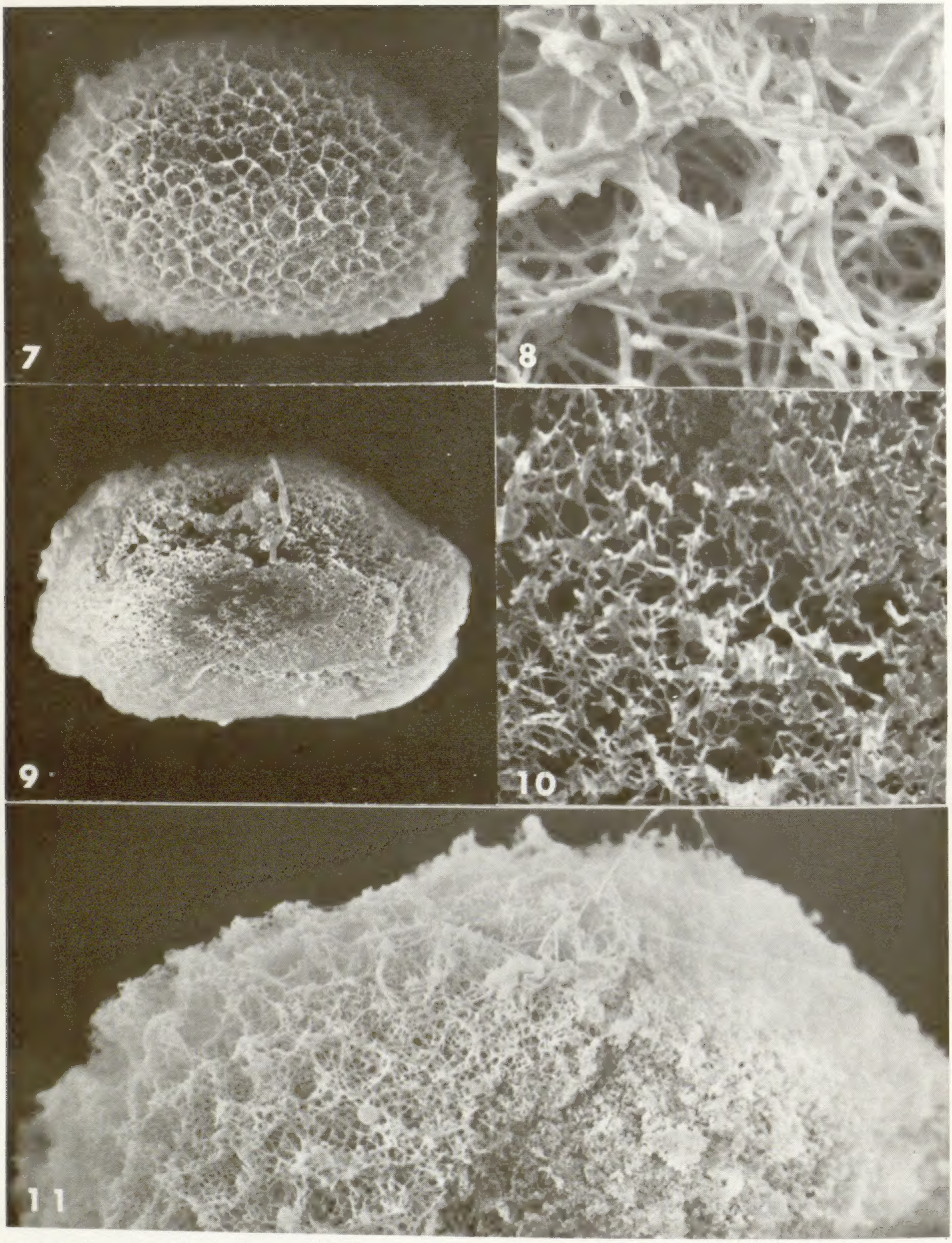
S. unisora: Kauai: *Heller 2863* (GH).

RESULTS

All *Sadleria* spores are bilateral, monolete, somewhat concave-convex in lateral view, and ovate in polar view. The external spore wall appears to be composed of several distinct layers. Light microscopy and scanning electron microscope studies indicate that the innermost layer in all species is smooth and without ornamentation and probably represents the exospore (*Figs. 3* and *14*). On top of this innermost layer are found one, two, or possibly three additional layers of spore wall, which in most species are loosely attached and easily separated from the exospore (*Figs. 3* and *14*). Since the outer layers are easily fractured and are not tightly affixed to the inner exospore, it is most likely that they represent a perispore, although it has not been possible to demonstrate that they are deposited from without the spore. However, in this paper the innermost smooth layer will be referred to as the exospore and the outer loosely attached layers as the perispore. Spore sizes without perispore in *S. cyatheoides*, *S. pallida*, *S. hillebrandii*, and *S. souleyetiana* are similar: 42.0–70.0 (mean = 53.5) μm long and 26.0–45.0 (mean = 35.4) μm wide. Spores of *S. squarrosa* and *S. unisora* are significantly larger, however: 58.0–81.0 (mean = 67.5) μm long and 37.0–56.0 (mean = 45.2) μm wide.

Spores of *S. hillebrandii* are illustrated in *Figs. 1, 2,* and *13*. The exospore surface is smooth. The perispore appears to consist of a single layer; however, some spores possess what appear to be remnants of an inner layer similar to that of spores of *S. cyatheoides*. The perispores are 2.4–4.4 (7.5) μm thick and are multitiered as in *S. cyatheoides* (*Fig. 13*). Generally, the surface of the perispore appears to be composed of a series of thin, irregularly sized and shaped plates. This surface pattern overlaps a substructure of small, crowded, irregularly oriented rods, seen in cross-section in *Fig. 13*. The inner surface of the perispore is minutely roughened. The spores of *S. pallida* that were examined were found to be similar in nearly all respects to those of *S. hillebrandii*.

Spores of *S. cyatheoides* are illustrated in *Figs. 3, 4,* and *12*. The exospore surface is smooth (*Fig. 3*). The perispore consists of at least two different lami-



Sadleria spores. FIG. 7. *S. unisora, Heller 2863* (GH), × 850. FIG. 8. *S. unisora*, surface view, *Heller 2863* (GH), × 8000. FIG. 9. *S. squarrosa, Grether & Wagner 3924* (US), × 1000. FIG. 10. *S. squarrosa*, surface view, *Grether & Wagner 3924* (US), × 5000. FIG. 11. *S. squarrosa*, surface view, *Munro 940* (NY), × 1200.

nated layers, an inner layer 0.5-1.0 μm thick, closely appressed to the exospore, and an outer layer. Light microscopy indicates that the total perispore thickness can be up to 10 μm. The outer surface of the outer layer is more or less smooth, with widely scattered and irregular perforations. An irregular deposition pattern with occasional areas showing the underlying rod pattern can be seen in *Fig. 4*. Connecting the outer and inner surfaces is a series of vertical rods (*Fig. 12*). The inner surface of the outer perispore layer appears to be smooth. The inner layer of perispore is thin and roughened on the external surface (*Fig. 12*). In some spores there is evidence that a third perispore layer exists, internal to the above two layers and overlying the exospore. This layer appears to be very membraneous and less ornamented than the layers above.

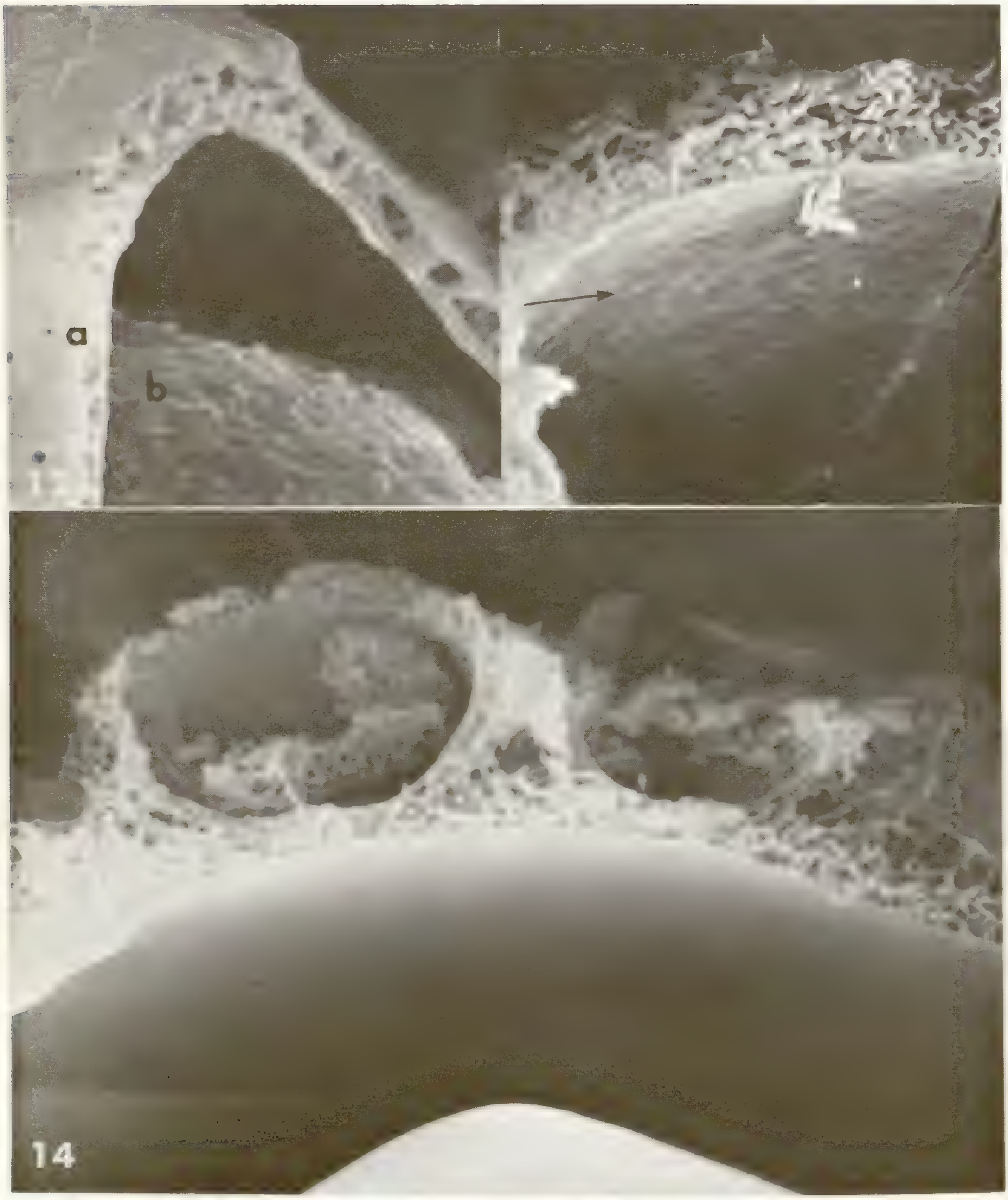
Spores of *S. souleyetiana* are illustrated in *Figs. 5*, *6*, and *14*. The exospore is smooth. The perispore in surface view is highly irregular and tuberculate (*Fig. 5*). The external surface is composed of an irregular and incomplete matrix, through which project numerous, irregularly oriented rods (*Fig. 6*). In some specimens, the matrix is nearly lacking. In cross-section, the perispore is seen to be composed of a single layer, with each tubercle enclosing a large lumen (*Fig. 14*). The interior of the perispore is composed of densely packed irregularly oriented and anastomosing rods. The outer surface of the perispore is variable in different spores. In some spores, the surface consists of irregular deposits between the papillate reticulum (*Fig. 6*); in other spores the deposits are lacking and the surface has a reticulate, areolate-papillate pattern. The perispores are 2.5-5.2 (13.3) μm thick.

Spores of *S. squarrosa* are illustrated in *Figs. 9-11*. They are more variable in surface pattern than are those of the other species investigated here. The perispore is apparently more tightly affixed to the exospore, as fractured walls were not observed. In the spores of some plants, the perispore is constructed of irregularly sized and shaped anastomosing rods arranged in a reticulum (*Fig. 11*). Spores of *S. unisora* are similar (*Figs. 7, 8*). In other plants, the reticulate pattern of rods and lumina is more minute and difficult to see (*Figs. 9, 10*). Frequently, there are regular deposits of matrix between rods and overlying much of the surface.

Spores from freshly collected specimens of *S. squarrosa* are brownish, but in much of the herbarium material examined the spores appear white, indicating perhaps that some change has occurred in the surface structure or that the material has been bleached out. Hillebrand (1888) indicated that spores of this species were pale, ". . . at first enveloped by a dense layer of soft clavate papillae, which disappear with age, leaving only a rough surface." Fresh spores have not been examined under the scanning electron microscope in this study.

DISCUSSION

Details of the spore wall that have been discovered using the scanning electron microscope have provided important features which may be used taxonomically to help delimit taxa in *Sadleria*. Four perispore types are present and correspond to *S. hillebrandii*, *S. cyatheoides*, *S. souleyetiana*, and *S. squarrosa*. The spores of *S. pallida* are almost identical to those of *S. hillebrandii*; although the former species is recognizable on other morphological grounds (Degener & Degener,



Sadleria spores. FIG. 12. *S. cyatheoides*, cross-section of outer perispore (a) and surface of inner perispore layer (b), *Degener 18502* (GH), × 6300. FIG. 13. *S. hillebrandii*, cross-section of perispore (arrow indicates inner surface), *St. John et al. 18447* (MICH), × 5000. FIG. 14. *S. souleyetiana*, cross-section of perispore, *St. John 24727* (MICH), × 5000.

1974), spore structure indicates a very close relationship to *S. hillebrandii*. Spores of *S. unisora* are nearly identical to spores of some plants of *S. squarrosa*, reinforcing the hypothesis that *S. unisora* is at best only an isolated form of *S. squarrosa*. The morphological features of *S. squarrosa* make it one of the most distinct and easily characterized species in the genus. The spore variation in this species may be due to ontogenetic processes or may indicate divergence in various populations.

Spore diversity in *Sadleria* could lead to a hypothesis that the genus is polyphyletic. However, the spores do have several features in common: a perispore which is composed of small rods which are arranged either in a regular reticulations (in *S. squarrosa* and *S. unisora*) or are more irregularly arranged (in the remaining taxa). The basic difference between spores, with the exception of the laminate perispore of *S. cyatheoides*, is the outer surface pattern of the perispore itself. The multi-layered perispore of *S. cyatheoides* is apparently unique to the genus, although fractured spores of *S. squarrosa* have not been observed.

It can be hypothesized that the basic spore type in the genus is that of *S. cyatheoides*. From this type, by loss of the inner perispore layer and by progressive loss of outer surface deposits, the surface pattern of *S. squarrosa* spores has been produced.

Investigation of spores from plants thought by Degener (pers. comm.) to be hybrids between *S. cyatheoides* and *S. hillebrandii* reveals perispore features which are intermediate between the two species. The outer perispore surface of individual spores exhibits both the irregular plates of *S. hillebrandii*, as well as the smooth surface of *S. cyatheoides* spores, thus supporting Degener's conclusions.

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Loxsomopteris anasilla, a New Fossil Fern Rhizome from the Cretaceous of Maryland

JUDITH E. SKOG*

A fusinized fern rhizome from the Lower Cretaceous beds of the Patuxent Formation (Potomac Group) in College Park, Maryland, is here described as a new genus and species. This rhizome is the first from a locality that was uncovered after the flooding of tropical storm Agnes in 1972.

Locality and stratigraphy.—In June 1972, flooding that followed a tropical storm uncovered Cretaceous clays containing plant remains in College Park, Maryland, near Washington, D.C. The predominantly grey to dark grey color, sandy lithology, and mica content of the outcrop, as well as its geographic position to the west of overlying Arundel and Patapsco strata, indicate its placement in the Patuxent Formation (L. J. Hickey, pers. comm.), the lowest of the three of the Potomac Group. A preliminary examination of a pollen preparation from the fossil-bearing bed is consistent with its placement in Zone I of the Brenner (1963) and Doyle (1969) classifications. The age of this zone is probably Aptian, but may range into the Barremian (*Fig. 1*).

Materials and methods.—Many fossils of gymnosperms and ferns corresponding to forms described by Fontaine (1889) and Berry (1911) occur in the clay lens, mainly as small fragments. Although some fragmentation probably occurred prior to fossilization, numerous planes of slippage (slickensides) in the clay are evidence of internal motion subsequent to burial.

The clay material containing the plants was maintained in a wet condition until further preparation was possible. It was bulk macerated in hydrofluoric acid. Larger plant fragments were sieved out; then the smaller fragments were sorted under a dissecting microscope. Some of the remaining residue was centrifuged and prepared for pollen and spore analysis. Fragments for sectioning were embedded in plastic, either in Epon 812 (50% A and 50% B mixture) or in Spurr Firm Embedding Medium. Sections were cut on a rotary microtome and mounted on microscope slides in Canada balsam. Observations and photographs were made using a Wild M-5 microscope and a Nikon S-Kt microscope with a combination of transmitted and reflected light. Photographs utilized Kodak Plus-X Pan film.

Description.—The well-preserved rhizome is approximately 2 cm long and 5 mm in diameter, with several roots (2.6 mm in diam.), two nodes, and a covering of hairs (some pointed and some blunt) that is more dense at the nodes. The carbonized remains of the rhizome are preserved as fusain (Schopf, pers. comm.) of a type not derived through fire (Schopf, 1975). The cell walls are opaque, brittle,

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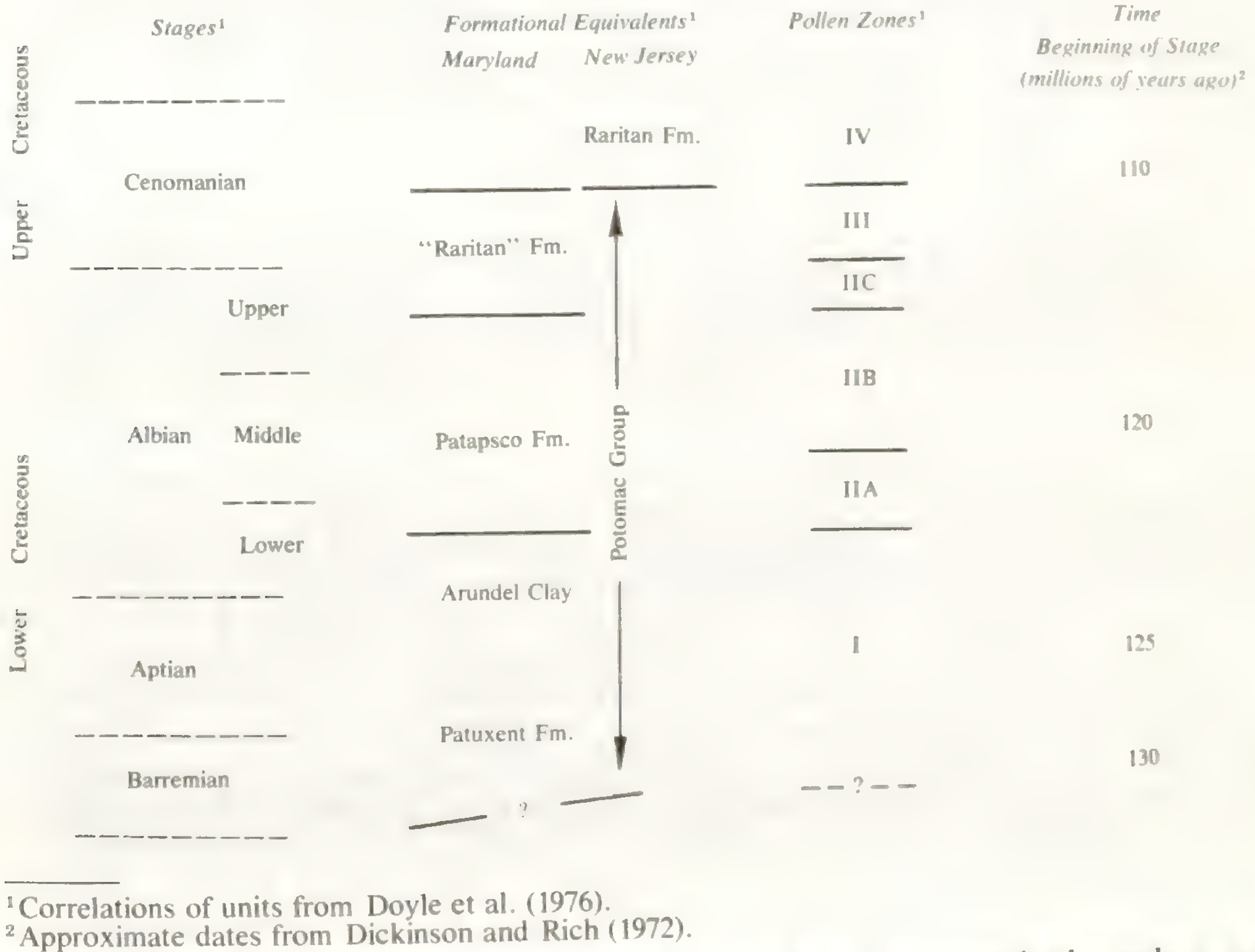
[1]The author is deeply indebted to Dr. Francis M. Hueber, Division of Paleobotany, Smithsonian Institution, for support and encouragement in all phases of the study, to Dr. Leo J. Hickey of the same department for information on the Cretaceous deposits in the area, and to the Division of Paleobotany for providing the laboratory space for the research. She also thanks Charles R. Parker for his assistance with the photographs.

glistening, and show smooth, conchoidal fractures, corresponding to Schopf's (1948) description of fusinized plant tissues. During the dehydration process for embedding in plastic, many of the brittle hairs lost their pointed tips, but the multicellular, bulbous bases remained and can be seen in section (*Fig. 3*). Some sections show the uniseriate tips of the hairs (*Fig. 5*). The cells of the hairs measure 16-33 μm in diameter.

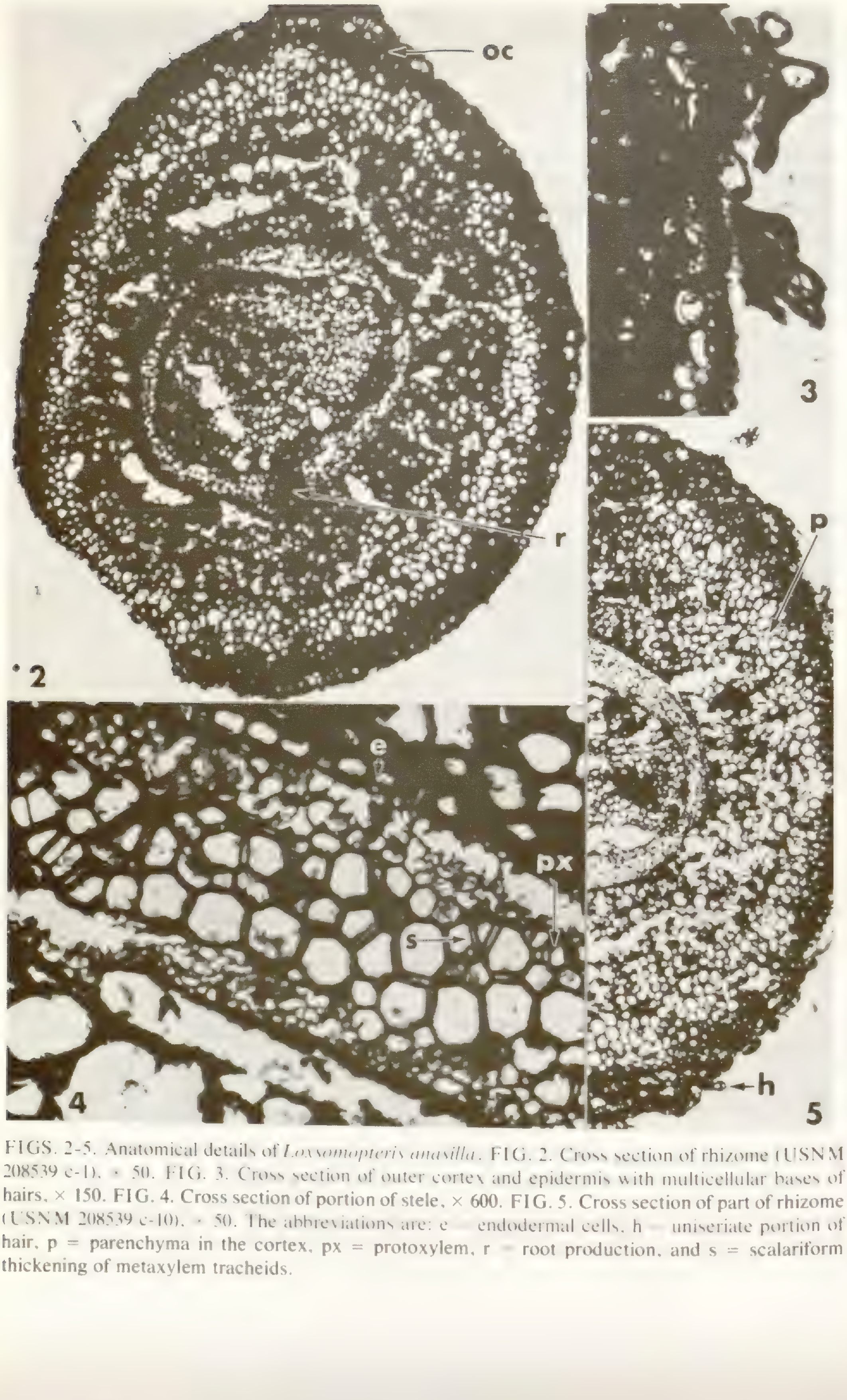
In section the rhizome is solenostelic with a sclerotic pith (cells 16-33 μm in diam.). The xylem is well preserved and is composed of scalariform tracheids (*Fig. 4*), protoxylem tracheids 12-17 μm in diam., and metaxylem tracheids 18-30 μm in diam. Maturation of the xylem is exarch with the protoxylem surrounding

FIG. 1. Stratigraphic relations of the Potomac Group in Maryland.



[1] Correlations of units from Doyle et al. (1976).
[2] Approximate dates from Dickinson and Rich (1972).

this tissue (*Fig. 4*). The phloem (cells 5-8 μm in diam.) surrounds the xylem and contains parenchyma cells 7-12 μm in diam. There is an endodermis of rectangular cells 8-12 μm in diam. around the stele, although this tissue is poorly preserved and difficult to distinguish (*Fig. 4*). The cortex is composed of an inner layer of mixed sclerenchyma (cells 13-23 μm in diam.) and parenchyma (cells 26-46 μm in diam.) and an outer layer of dense sclerenchyma (*Fig. 2*). The epidermis is a layer of isodiametric cells with hairs arising from them. The roots appear to arise from the protoxylem area and become diarch as they pass through the cortex (*Fig. 2*). Petiole traces are poorly preserved, but appear C-shaped and produce a gap in the stele as they are formed. No petiole traces are preserved outside the cortex.



FIGS. 2-5. Anatomical details of *Loxsomopteris anasilla*. FIG. 2. Cross section of rhizome (USNM 208539 e-1). × 50. FIG. 3. Cross section of outer cortex and epidermis with multicellular bases of hairs. × 150. FIG. 4. Cross section of portion of stele. × 600. FIG. 5. Cross section of part of rhizome (USNM 208539 e-10). × 50. The abbreviations are: e = endodermal cells, h = uniseriate portion of hair, p = parenchyma in the cortex, px = protoxylem, r = root production, and s = scalariform thickening of metaxylem tracheids.

Loxsomopteris J. E. Skog, gen. nov.

Fern rhizome covered with bristle-like hairs, these multicellular at the base and tapering to a uniseriate tip, with a sclerotic pith, solenostele, exarch xylem maturation, and a cortex of mixed parenchyma and sclerenchyma (*Fig. 2*).

TYPE: *Loxsomopteris anasilla* J. E. Skog.

Loxsomopteris anasilla J. E. Skog, sp. nov. **Figs. 2-5.**

Rhizome dorsiventral, terete in cross section, solenostelic, covered with bristle-like hairs; hairs multicellular at the base, tapering to a uniseriate tip; outer cortex sclerenchymatous, inner cortex of sclerenchyma and parenchyma; endodermis present; xylem of scalariform tracheids, maturation exarch with protoxylem area around the periphery of the tissue; phloem with sieve elements and parenchyma surrounding the xylem; pith sclerotic; petiole traces C-shaped; roots diarch.

TYPE: United States National Museum 208539, a, b, and c 1-21, series of mounted slides, all deposited in the Paleobotany Collections, U. S. National Museum of Natural History.

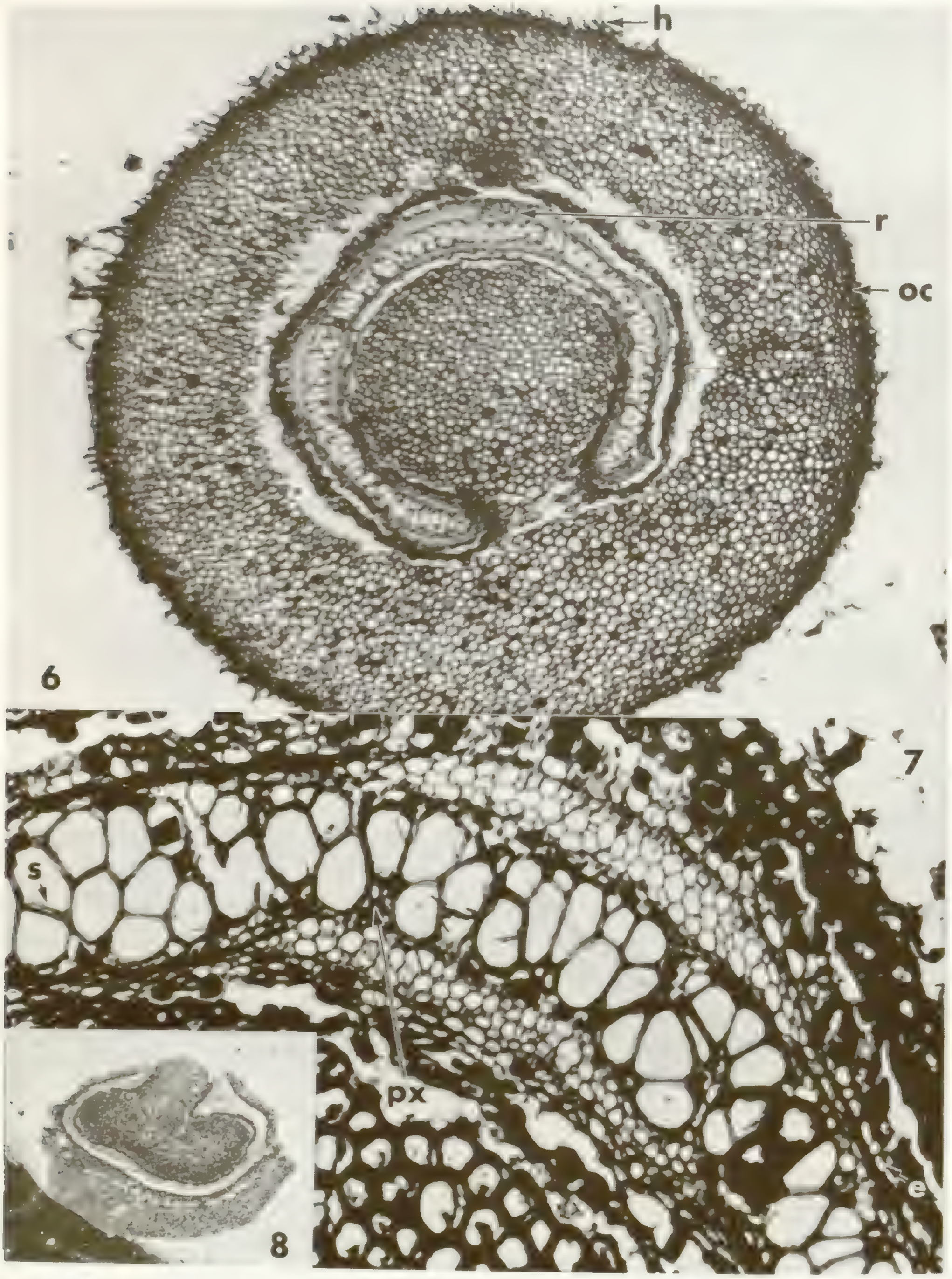
TYPE LOCALITY: Paint Branch, 39°00′ N Lat., 76°56′ W Long., on the creek bank 500 ft NW of the intersection Greenbelt Road and Route US-1, College Park, Maryland, U. S. A.; USNM locality 14212.

STRATIGRAPHY: Lower Cretaceous Barremian or Aptian, Potomac Group, Patuxent Formation.

DERIVATION OF THE EPITHET: From the Greek *anásillos*, meaning with bristling hairs.

The amphiphloic siphonostele, exarch maturation of the xylem, scalariform tracheids, sclerenchymatous pith, mixed cortex, size of the stem, and relative age relate *L. anasilla* to the form genus *Solenostelopteris* Kershaw (1910). Based upon her description and a reexamination of the type material in the British Museum (Natural History) Paleobotany Collection (*Fig. 8*), *Loxsomopteris* differs from *Solenostelopteris* in cortical arrangement of sclerenchyma and parenchyma, presence of epidermis, age, locality, and size. The outer cortex and epidermis of *S. japonica* are not present, and so there is no indication of hairs on the type species. Kershaw (1910) suggested possible relationships with the Davallieae and, in particular, the extant fern genus *Microlepia*. Her opinion was based on the distribution of sclerenchyma in the cortex, the arrangement of the xylem and phloem, and the marginal thickening of the xylem in forming the leaf gap.

A second species of *Solenostelopteris* was described by Ogura (1930) from the Upper Cretaceous of Japan as *S. loxsomoides*. This species and *L. anasilla* appear to be closely related, particularly in the possession of hairs on the epidermis. The hairs of *S. loxsomoides* are conical, multicellular, and arise from the outer cortex, which is composed of large, thin-walled cells. Ogura's diagram and illustration together do appear to show this sort of structure; however, the question arises as to whether the protrusions are hairs. The epidermis is not clear from the illustration, and if these are truly hairs it is unlikely that the cortex would participate as extensively in their formation as has been illustrated. Thus, although *S. loxsomoides* may very well belong in the new genus *Loxsomopteris*, it



FIGS. 6-8. Anatomical detalis of *Loxsomopsis* and *Solenostelopteris*. FIG. 6. Cross section of *L. costaricensis* (*Mickel 3001*, US). × 11. FIG. 7. Cross section of portion of stele of *L. costaricensis*, with the pith in the lower portion of the photograph. × 54. FIG. 8. Cross section of the type of *S. japonica*, specimen v-28872a (Stopes no. 1YA-21a). × 8. Same as Kershaw (1910, fig. 3); photograph courtesy of the British Museum (Natural History). The abbreviations are: e = endodermal cells; h = multicellular base of hair; oc = sclerenchymatous outer cortex, px = protoxylem, r = production of root, and s = scalariform thickening of metaxylem tracheids.

seems advisable to let it remain in the form genus *Solenostelopteris* until the type specimen has been reexamined. *Loxsomopteris* differs in having hairs with pointed tips arising from the epidermis, a sclerotic outer cortex, and is terete in cross section rather that elliptic. A further distinction between *S. japonica* and *L. anasilla* is that the inner cortex is composed of thick-walled cells in the former. Ogura suggested a close relationship with *Loxsoma* (Loxsomaceae), reflected in the specific epithet, based upon the indument and stelar pattern.

Two other species, *S. nipanica* and *S. sahnii*, were described by Vishnu-Mittre (1958) of Jurassic age from India, but neither of these was described as having hairs on the epidermis.

On the basis of locality, age, sclerotic outer cortex, and the characteristic hairs on the epidermis, the specimen from Maryland is described as a new genus in the family Loxsomaceae. The systematic position of *Loxsomopteris* is difficult to determine because of the lack of attached fronds. Further work on the pinnules found in the same deposit is continuing, and may eventually suggest a more certain relationship. On the basis of the epidermal appendages, relationship with Loxsomaceae is clearly suggested. Within that family, *Loxsomopteris anasilla* can probably be compared most closely with *Loxsomopsis costaricensis*. The hairs of the latter species are multicellular at the base tapering to uniseriate tips, and the points may break off leaving some hairs blunt with only the bulbous bases remaining (*Fig. 6*). Anatomically, the fossil is strikingly similar to the living fern (*Fig. 7*) in the solenostele, sclerenchymatous pith, mixed cortex with the outer layer of sclerenchyma, exarch maturation of the xylem with protoxylem areas around the xylem, similar production of diarch roots, and C-shaped petiole trace at its point of origin. However, because no attachment to fronds is yet available, one must not ignore other possible living relatives of *Loxsomopteris*, although the similarities are not as close to any other genus of extant ferns which has a solenostelic vascular system. According to Gwynne-Vaughan (1903, p. 727), the exarch protoxylem seems to limit comparison to *Loxsoma*, *Dicksonia* [*Dennstaedtia*] *apiifolia*, *Davallia platyphylla*, *D. speluncae*, *D. hirta*, or *D. marginalis*. The genus *Davallia* can be eliminated from comparison because of the presence of paleae instead of hairs, and *Dennstaedtia* does not possess the bulbous-based hairs (Bower, 1926). In Loxsomaceae the characteristic islets of parenchyma in the cortex (Gwynne-Vaughan, 1901) are further evidence of the affinities *Loxsomopteris anasilla* has with this family.

The new fossil fern rhizome indicates that the anatomical characteristics typical of the family Loxsomacae apparently were present in the Lower Cretaceous. However, there is no spore record of this family—or the available spores may not be distinctive enough to determine family relationships. Brenner (1963, p. 31) attributes fern spores of this age to the Matoniaceae, Cyatheaceae, Gleicheniaceae, Schizaeaceae, and Osmundaceae. He interprets the paleoecology of the region as a warm-temperate, broadleaf evergreen rainforest and suggests that these fern families are not inconsistent with this environment. Doyle (1969), on the other hand, suggests the possible presence of Cyatheaceae, Schizaeaceae, and Gleicheniaceae in the Lower Cretaceous, but attributes all

other spores to "groups of less certain affinities," an interpretation which is probably more accurate because trilete spores are found in many families of pteridophytes. Information from the leaf and pinnule types of the Lower Cretaceous must be interpreted with caution, since most of the work on these beds by Fontaine (1889) and Berry (1911) was based upon compression fossils without critical comparative study. Details of leaf anatomy have not yet been investigated, but further work in progress will likely yield a reinterpretation of the groups present.

Previous descriptions of these fossil beds in the Potomac Group (Fontaine, 1889; Berry, 1911) have dealt mainly with compression material. Only the fern *Tempskya* from the Patapsco Formation has been found as a petrifaction (Berry, 1911, p. 295). This rhizome of *L. anasilla* is therefore interesting, as it is the earliest fossil fern stem from the Lower Cretaceous yet found in Maryland.

That the most closely related species are from the Upper Cretaceous of Japan indicates further evidence of the relationship of eastern Asiatic and eastern North American floras since the Cretaceous. Li (1952) indicates that there are few extant ferns that show this relationship (*Camptosorus*, *Osmunda*, *Onoclea*), possibly because of the production of spores rather than seeds as a dispersal mechanism. Correlation may prove to be closer when ages of Cretaceous continental beds are better defined for Asia and America.

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A New Species of Hymenophyllum from Central America

ROBERT G. STOLZE*

The Filmy Fern genus *Hymenophyllum* includes an interesting and closely knit complex of species, treated by C. V. Morton (1947) as sect. *Sphaerocionium*, subsect. *Lanata*. Morton (1968) revised the classification of Hymenophyllaceae and placed this group in subg. and sect. *Sphaerocionium*, subsect. *Hirsuta*. The latter is distinguished by the following characteristics: segment margins entire rather than toothed; blades bearing stellate trichomes on the leaf surface between, as well as on, the veins; and veins lacking accessory wings not in the same plane as the leaf. The group contains 20-25 species, which occur chiefly in the neotropics.

While studying subsect. *Hirsuta* for "The Flora of Guatemala," I came upon a new species of *Hymenophyllum* represented by specimens previously undetermined or misidentified as *H. sieberi* (Presl) v. d. Bosch or *H. trapezoidale* Liebm. A few of those determined as *H. sieberi* had been annotated by Morton; perhaps he (1947, p. 180) was referring to these when he said, "Some of the Guatemalan specimens are more or less aberrant."

Hymenophyllum crassipetiolatum Stolze, sp. nov. **Figs. 1, 3.**

Rhizoma repens; folia indeterminita, 12-42 cm longa, 3-8(10) cm lata; petioli 4-11(16) cm longi, (0.5)0.6-0.9 mm crassi, non alati; laminae anguste lanceolatae vel ovatae, rhachidibus late alatis, rarius ad basin non alatis; pinnae plerumque bipinnatifidae, late alatae; pinnulae pinnatifidae, pinnulae apicales bifidae vel simplices; segmenta ultima integra; trichomata in venis et in superficiebus foliorum stellata, sessilia, trichomata marginalia radiis 4-6 plerumque adpressis et versus apicem segmenti flexis; indusia saepe latiora quam longa, trichomatibus simplicibus vel bifurcatis instructa.

TYPE: Slopes of Volcán Gemelos, Dept. Zacapa, Guatemala, 1942, *Steyermark 43302* (US; isotypes F, GH).

Pendent from tree trunks, or growing on moist banks, in deep shade in cloud forests, 1,250-3,300 m. Known from Mexico (Chiapas), Guatemala, Honduras, and El Salvador.

Rhizome wiry, long-creeping, provided with simple, reddish to light brown trichomes; leaves subdistant on the rhizome, indeterminate, pendent, mature ones 12-42 cm long, 3-8(10) cm wide; petiole 4-11(16) cm long, (0.5)0.6-0.9 mm in diameter, nonalate (although the basal pinna sometimes short decurrent), sparsely to abundantly provided with simple, bifid, or (mostly) stalked, stellate trichomes; lamina ovate or, more commonly, narrow-lanceolate, not reduced at base, or the lower 1-4 pairs of pinnae somewhat shorter; rachis broadly alate throughout, or nonalate at the base, the wings plane to slightly crispate, sparsely or abundantly provided with sessile or subsessile, stellate trichomes; pinnae commonly bipinnatifid, the costae broadly alate; pinna segments 4-12 pairs, the larger ones deeply pinnatifid, the apical ones bifid to simple, ultimate segments plane or slightly

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FIG. 1 Holotype of *Hymenophyllum crassipetiolatum*, *Steyermark 43302* (US).

undulate, entire, veins and leaf surfaces sparsely to abundantly provided with sessile-stellate trichomes; marginal trichomes abundant, sessile-stellate (rarely minutely stalked), most of the 4-6 stout rays commonly appressed and directed toward the segment tip; indusium as broad or broader than the ultimate segment, not or scarcely immersed in the segment tip, the valves as broad or broader than long, their margins provided with simple or bifurcate trichomes.

SELECTED SPECIMENS EXAMINED:

MEXICO: Chiapas: *Matuda 5233* (F). **GUATEMALA: Alta Verapaz:** Finca Los Alpes, ca. 4000 ft. *Wilson 352* (F). **Baja Verapaz:** Sierra de las Minas ca. 5 km S of Purulhá, 1600 m, *L. O. Williams et al. 41976* (F). **Chiquimula:** Cerro Brujo, SE of Concepción de las Minas, 1700-2000 m, *Steyermark 31034* (F, GH, US). **El Progreso:** Between Finca Piamonte and the summit of Volcán Sta. Luisa, 2400-3333 m, *Steyermark 43546* (F, US). **Zacapa:** Between Loma El Picacho and Cerro de Monos, 2000-2600 m, *Steyermark 42795* (F, US). **HONDURAS: Morazán:** Dry slopes of Mt. San Juancito, near El Rosario, 1400 m, *Molina 23402* (F). **Ocotepéque:** Mt. Cocal, 20 km NW of Ocotepéque, 1800 m, *Molina 22100* (F). **EL SALVADOR: Chalatenango:** East slope of Los Esemiles, ca. 2430 m, *Tucker 1062a* (F). **Santa Ana:** Montaña Montecristo, 2100 m, *Molina & Molina 12488 (F).*

The comparatively thick petiole of this species is one of its most distinctive features. The petiole diameter of most *Hymenophyllum* species is less than 0.5 mm, and frequently is only 0.1-0.2 mm. Noteworthy also is its luxuriant, highly dissected leaf blade, which often attains lengths of over 40 cm. In larger primary segments (pinnules) of most pinnae, the veins are pinnately arranged, so that the pinnae are essentially bipinnatifid. (In more distal pinnae the primary segments are merely bifid or simple.)

Some other characteristics in *H. crassipetiolatum* are subtle, but important. The indusial valves vary somewhat in dimension, occasionally they are suborbicular or sometimes slightly longer than broad, but most commonly the valves of mature indusia are broader than long. The stellate trichomes of the segment margins are sessile (rarely very short-stalked), with 4-6 stout rays closely appressed along the margin and most of them bent toward the segment tip (*Fig. 3*). The marginal stellate trichomes of many similar species appear much more delicate and have long slender stalks with filiform rays that spread in a more random pattern. (*Fig. 2*).

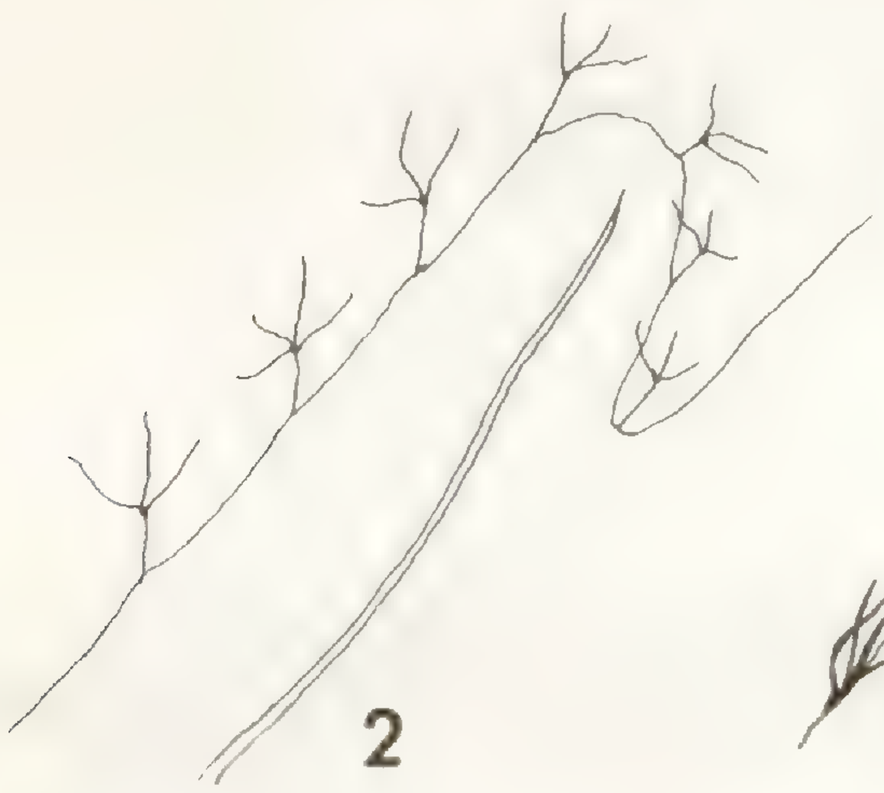
In Mexico and Central America, the affinities of *H. crassipetiolatum* are with *H. sieberi*. The two may be readily separated by a number of characteristics, including those in the following key:

Petioles (0.5)0.6-0.9 mm in diam, not alate; pinnae essentially bipinnatifid; marginal trichomes stout, stellate, sessile, the rays mostly appressed and bent toward the segment tip; indusial trichomes simple to forked; indusia mostly broader than long; plants growing at 1,250-3,300 m altitude. ..... *H. crassipetiolatum*

Petioles 0.3-0.5 mm in diam., alate at the apex or in the upper half; pinnae essentially pinnatifid; marginal trichomes delicate, stellate, stalked, the rays spreading; indusial trichomes forked to stellate; indusia mostly longer than broad; plants growing at 950-1,600 m altitude... *H. sieberi*

Although *H. crassipetiolatum* frequently has been identified in herbaria as *H. trapezoidale*, the two belong to different subsections. The blades of the latter are glabrous between the veins and the margins, the rachises are nonalate in the lower portion of the blade, and the marginal trichomes are simple, bifurcate, or stalked-stellate with 3 delicate rays.

Three South American species perhaps are more closely related to *H. crassipetiolatum* than any of the Central American species: *H. lindenii* Hook., *H. interruptum* Kunze, and *H. plumieri* Hook. & Grev. *Hymenophyllum lindenii* is one of the few with petioles nearly a full millimeter in diameter, but the rachis is nonalate in the lower portion of the blade and indusial trichomes are predominantly stalked-stellate, whereas those of *H. crassipetiolatum* are simple or bifurcate. Both *H. plumieri* and *H. interruptum* have more delicate petioles and their blades are less highly dissected. The latter has groups of fertile pinnae often separated by several sterile ones, and *H. plumieri* has the petiole alate at the apex.



FIGS. 2-3. Trichomes on segment margins of *Hymenophyllum*. FIG. 2. *Hymenophyllum sieberi*. FIG. 3. *Hymenophyllum crassipetiolatum*.

In spite of Morton's past work with the family and genus, *Hymenophyllum* still poses many interesting problems in taxonomy. The plants are small and often inconspicuous, and grow primarily in the deep, dense forests, so undoubtedly there will be new discoveries as additional collections are made.

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Uncommon Wall Thickenings in the Sieve Cells of Pteris wallichiana

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Pteris wallichiana Agardh was collected from Kerala, India, fixed in FAA, and processed for microtomy by conventional methods (Sass, 1958). Sections were stained following Cheadle, Gifford and Esau (1953). In addition, I_2KI and H_2SO_4 was used for cellulose, the PAS reaction for insoluble polysaccharides (Jensen, 1962), and Toluidine blue 'O' for cell walls (O'Brien, Feder & McCully, 1964).

During our study of phloem structure in *Pteris wallichiana* we observed uncommon papillose thickenings on the walls of sieve cells, rarely in the rhizome and frequently in the rachis. These sieve cells were randomly distributed and generally belonged to the metaphloem. Sieve cells with this thickening did not appear to be structurally different from other sieve cells. The thickenings project 2.4-10.4 μm from the sieve cell wall into the cell lumen (*Figs. 1-2*). Phloem parenchyma cells having a common wall with sieve cells rarely show this type of thickening (*Fig. 4*). The thickening may be on only one side of the common wall or it may be on both sides of the wall of two adjacent sieve cells. Occasionally small fissures, some of which may be artifacts, appear in the papillose thickenings, which cause the thickening to appear to consist of different parts (*Figs. 5-8*). The thickenings are neither tyloses nor, apparently, a reaction to fungal infection. The thickenings are PAS-positive and give a confirmatory test for cellulose. They stain purple red with toluidine blue 'O', a staining reaction similar to the remaining part of the sieve cell wall. A membraneous lining is sometimes observed over the thickenings (*Fig. 3*).

Similar wall thickenings have not been reported in sieve elements of other fern species. Warrington (1970) reported papillose cellulose thickenings of cell walls in the cortical cells of rhizome of *Geocaulon lividum* (Santalaceae), a dicotyledonous plant, but these thickenings were always in pairs on common cell walls.

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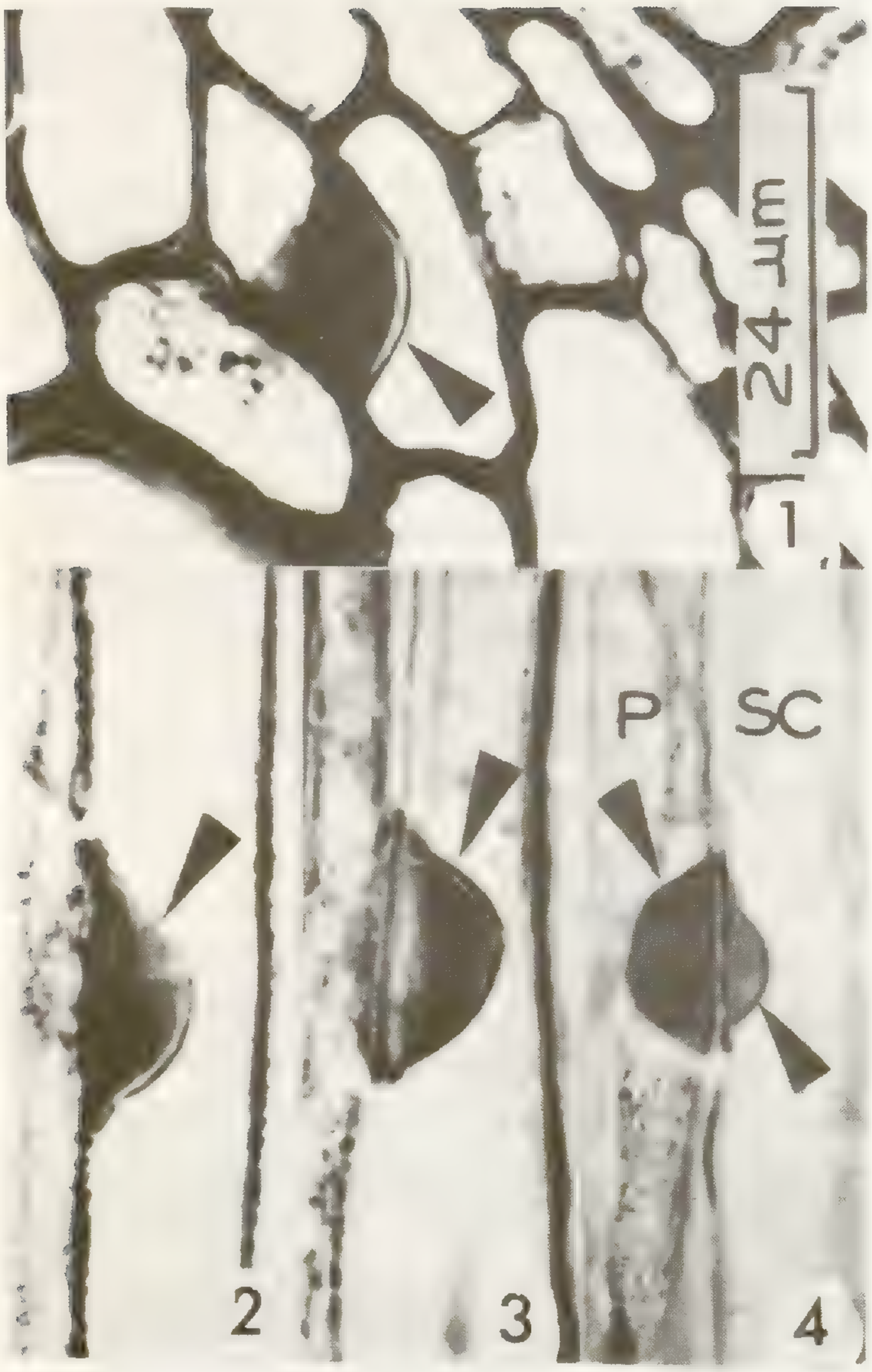

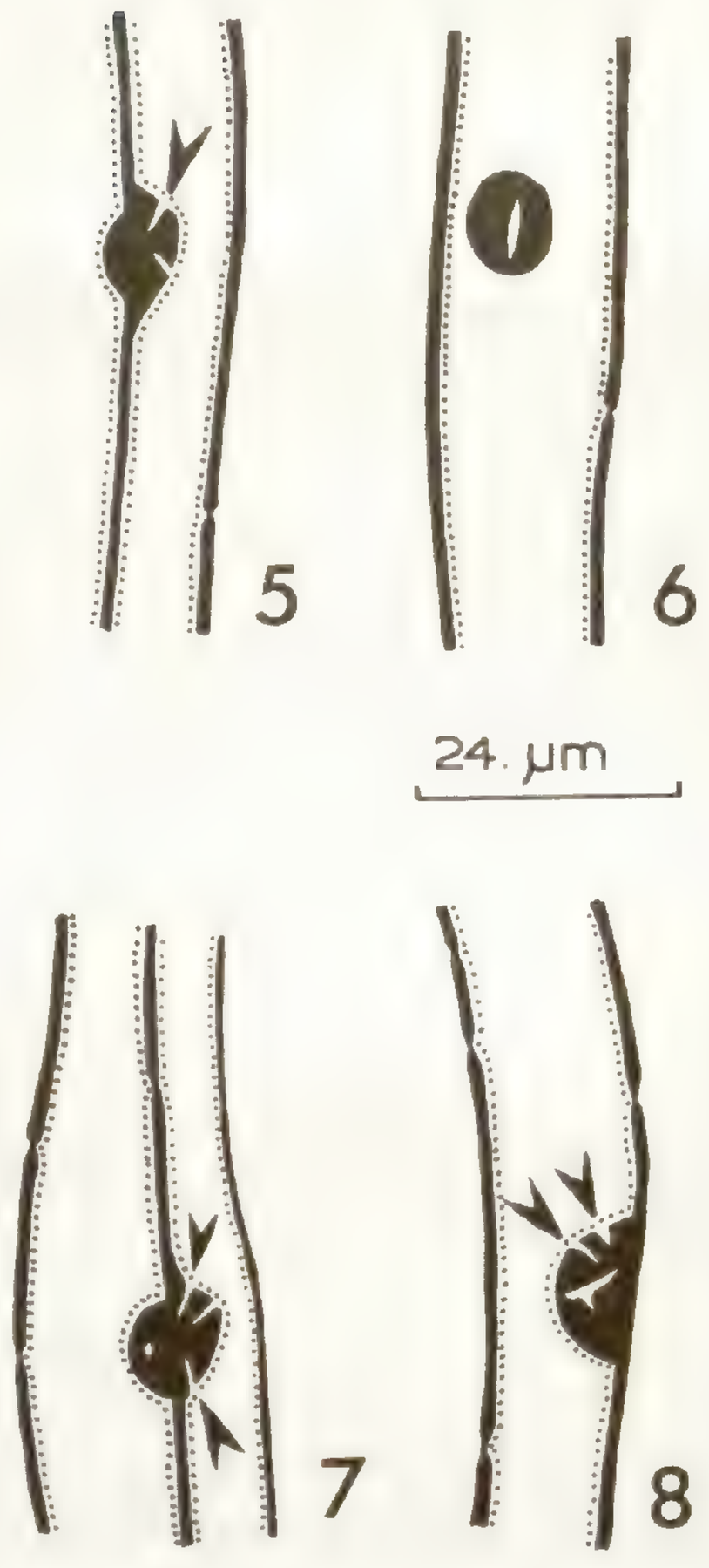

FIGS. 1-4. Rachis phloem of *Pteris wallichiana*. FIG. 1. Transection showing sieve cells with and without wall thickenings. FIG. 2. Longisection of a portion of a sieve cell showing a thickening. FIG. 3. Longisection of a portion of a sieve cell showing a thickening with membranous lining. FIG. 4. Longisection of a portion of a sieve cell and a phloem parenchyma cell showing paired thickening along the common wall. P = phloem parenchyma, SC = sieve cell. FIGS. 5-8. Longisections of portions of sieve cells showing a variety of fissures in the thickenings.

Some Lesser Known Ferns from the Western Himalayas, 1. Cheilanthes anceps var. brevifrons

S. P. KHULLAR*

Nearly a century ago Blanford (1886) recognized two new species in the *Cheilanthes farinosa* (Forsk.) Kaulf. complex: *C. anceps* Blanf. and *C. grisea* Blanf. Later, Blanford (1888) reduced these species to varieties of *C. farinosa*. Hope (1901), Alston (1956), and Verma (1964) considered these taxa to be species. Panigrahi (1962) regarded the tetraploid occurring in Ceylon as *Aleuritopteris anceps* (Blanf.) Panigr. and the diploid as *A. grisea* (Blanf.) Panigr.

Hope (1900, p. 250) apparently was the first to point out that *C. anceps* had two forms. His specimens, from near Simla in the western Himalayas, although collected at the same time as Blanford's, differed in being smaller, more delicate, and sometimes in having apparently concolorous rhizome scales. This led Hope to comment that his specimens seemed near to *C. farinosa* var. *grisea* (Blanf.) Blanf. These small specimens cannot be *C. grisea*, however, because that species has a naked rachis, always has concolorous, brown scales that are restricted to the stipe bases, and has a crenate or irregularly lobed indusial margin. *Cheilanthes anceps*, on the other hand, is characterized by its lanceolate to oblong-lanceolate fronds, scaly stipes and rachises, and lacerate indusial margins.

Sufficient morphological and cytological differences occur between the two types of *C. anceps* to require their separation into varieties, but I hesitate to assign the rank of species to the two because of certain resemblances between them. In both, bicolorous scales are present on the stipe and rachis, the fronds are more or less lanceolate, and the indusial margin is always lacerate.

Cheilanthes anceps Blanf. var. anceps. **Fig. 1.**

Fronds 25–48 cm long; stipes 10–20 cm long, 0.75–1.5 mm in diam., with a sulcate stele, approximately equalling the laminae, dark chestnut to almost black, glossy, the stipe scales linear-lanceolate, bicolorous, dark with pale margins; rachis scales similar; laminae 10–24 cm long, (2.5) 3–4.5 cm wide, lanceolate to oblong-lanceolate, thin, not compact, heavily white-waxy beneath, the lowest 2 or more pinna pairs subequal, rather distant; indusia narrow, toothed or lacerate. $n=29$ in material from Darjeeling, eastern Himalayas (Verma in Mehra, 1961).

SPECIMENS CITED:

INDIA: Himachal Pradesh: Simla Hills, 650 m, 15 Sept 1960, *S. S. Bir* (PAN 4266-69). **Uttar Pradesh:** Mussoorie, Jamna Bridge, 600 m, 27 Aug 1959, *S. S. Bir* (PAN 2639-40); Nainital, Kathogodam Road, 1200 m, 5 Oct 1975, *S. P. Khullar 24* (PAN). **West Bengal:** Darjeeling, Manjitar-Teesta Road, Aug 1951, *S. C. Verma* (PAN 3776-3779).

This variety occurs at 600–1800 m altitude in the western Himalayas and at about 150–450 m altitude in the eastern Himalayas.

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FIG. 1. *Cheilanthes anceps* Blanf. var. *anceps (S. S. Bir,* PAN 2639).

FIGS. 2-4. Holotype of *Cheilanthes anceps* var. *brevifrons* (*S. P. Khullar*, PAN 5977). FIG. 2. Entire specimen. FIG. 3. Indusial lobe showing highly lacerate margin. × 38.5. FIG. 4. Bicolorous stipe scale, × 20.

Cheilanthes anceps var. brevifrons Khullar, var. nov. **Figs. 2-4.**

A *C. ancepiti* var. *ancepiti* statura minore, stela tereti, stipitibus pallidioribus, laminis crassiusculis et chromosomatum numero differt.

Fronds (4)9-12.5(27) cm long; stipes (2)3.6-4.7(10) cm long, 0.3-0.8 mm in diam., with a terete stele, generally shorter than or equalling the laminae, light to dark brown, glossy; stipe scales narrowly linear-lanceolate, deciduous, abundant, bicolorous, brown at the center, paler towards the margin, more distinctly bicolorous near the stipe base than near the apex; rachis scales similar but smaller; laminae 5.5-8.0 cm long, 3-3.5 cm wide, thick, compact, more or less oblong-lanceolate, the apex acuminate, the basal pinna pair shorter than the suprabasal pair, the basal basiscopic pinnule pair divergent and nearly parallel to the stipe; pinnae subopposite, divergent, the lower 2 or 3 suprabasal pairs equal and distant compared with those in the proximal half of the lamina; pinnules obtuse, ascending, lobed; indusia narrow, generally regularly lobed, not continuous, brown, the margin deeply and regularly lobed with long, marginal teeth; spores brown, globose, the exine with reticulate thickenings appearing like marginal projections, 50-70 um × 45-65 um; $n=30$ in material from the western Himalayas (Khullar & Mehra, 1973).

HOLOTYPE: Taradevi, Simla, Himachal Pradesh, India, 1800 m, July 1967, *S. P. Khullar* (PAN 5977).

PARATYPES:

INDIA: Himachal Pradesh: Simla Hills, Kasauli, 1800 m, July 1967, *S. P. Khullar* (PAN 6053-6068, 6492); Tuti Kundi, 1500 m, 18 Aug 1960, *S. S. Bir* (PAN 3908-10); Dalhousie, Bathri, 1350 m, 16 Aug 1964, *M. Golaknath* (PAN 5166, 5291, 5530). **Uttar Pradesh:** Ranikhet, 1800 m, Sept 1972, *S. P. Khullar* (PAN 22).

This variety is quite common between 1300 and 1800 m altitude in the western Himalayas.

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SHORTER NOTES

A NEW LOCALITY FOR LYCOPODIUM SERRATUM IN MEXICO.—Until recently *L. serratum* had been collected only once in Mexico. Liebmann found it in the State of Oaxaca during the last century and published it as a new species, *L. sargassifolium*. His species has proven to be the same as *L. serratum*, which is distributed primarily in the Old World: temperate Asia, the Zonda Islands, New Caledonia, and Hawaii. It is scarcely represented in the New World: Cuba, Hispaniola, and Mexico. This is another example of an Asian–American disjunct distribution; the major range of *L. serratum* and the entire ranges of the species allied to it are in the Old World.

The second known Mexican collection of *L. serratum* was made by A. J. Sharp and Blanca Pérez García in June 1973 at a locality 6 km southwest of Tianguistengo, Municipio of Zacualtipán, in the State of Hidalgo, at an altitude of 2000 m. The plants were found in a subdeciduous forest with *Liquidambar styraciflua*, *Ternstroemia latifolia*, *Alchornea latifolia*, *Alnus*, and *Quercus*. The specimens of this collection were found in two small patches about 500 m apart, both near a small stream. Because of the dichotomous branching and the prostrate habit of the older stems, the plants have a circular outline; four series of dichotomies can be noted in the larger specimens. The leaves are in several spiral rows and characteristically have their margins irregularly toothed. The sporophylls are similar to the sterile leaves or are just a little smaller. Although strobili are not formed, there is a slight concentration of sporophylls along the stem.—*Ramón Riba and Blanca Pérez García, Universidad Autónoma Metropolitana-Iztapalapa, Apartado Postal 55-535, México, D. F., México, and Martha Pérez García, Instituto de Biología-Botánica, Universidad Nacional Autónoma de México, Apartado Postal 70-233, México, D. F., México.*

NATURALIZATION OF CYRTOMIUM FORTUNEI IN NORTH AMERICA.—The fern *Cyrtomium fortunei* Smith, a native of southeastern China, has become established in Charleston, South Carolina as an apparent escape from cultivation. This record presently represents the only known naturalization of the species in North America. Specimens were first noticed in 1973, growing in association with *Cyrtomium falcatum* (L. fil.) Presl, on a moist, north-facing brick wall in a cemetery in downtown Charleston. By 1975 the ferns had increased to a colony of about seventy plants, and a collection was made (*MacDougal 184* and *186*). The probable parent plant is growing nearby with nursery-raised *C. falcatum*, and was evidently brought to the graveyard with them.

In the living state this species is easily distinguished from *C. falcatum*, which it resembles, by the dull green, not glossy, upper side of the fronds. The pinnae are more numerous and smaller, lanceolate or oblong, 5–8 × 1–2.5 cm, acuminate, and have finely serrate margins.

It is especially interesting to record this naturalization in view of the success that *C. falcatum* has had in the Charleston area following its naturalization in the early 1940's; see K. W. Hunt's "Ferns of the vicinity of Charleston, S.C." (Charleston Museum Leaflet No. 17). Voucher specimens of *C. fortunei* have been deposited in several herbaria, including those of the New York Botanical Garden, The Smithsonian Institution, and The Charleston Museum. I wish to thank Dr. David B. Lellinger and Albert Giraldi of The U.S. National Herbarium for identifying this fern.—*John M. MacDougal, 1 New Town Lane, Charleston, SC 29407.*

FORKED FRONDS IN ASPLENIUM RHIZOPHYLLUM.—Forking of fern fronds is a common occurrence, but has not been reported for *Asplenium rhizophyllum* L. Buzz Darby, an amateur naturalist of Springfield, Missouri, has discovered several colonies of *A. rhizophyllum* in Newton County, Arkansas, in which some plants had a forked blade. The identity of two such colonies growing

FIG. 1. *Asplenium rhizophyllum* with blade forked at base (*Key 1238*, SMS). FIG. 2. *A. rhizophyllum* with blade forked (*Key 1239*, SMS).

along a creek bank on moss-covered sandstone boulders has been confirmed and vouchers made (*Key 1238, 1239*, SMS). Colonies with similarly forked blades have been found on limestone outcroppings in a mesophytic forest in Montauk State Park, Dent County, Missouri (*Maupin 1145*, SMS) and in a similar habitat near Eminence in Shannon County, Missouri, (*Key 1282*, SMS). My son has discovered a fourth location on limestone near the opening of the Ozark Underground Laboratory Cave in the xerophytic, forested hills of Taney County, Missouri.

In some plants, the stipe of the forked frond is unusually long (8 cm) and is triangular (1.5–2 mm on each side). Forking occurs 5 mm above the cordate base of the doubled, sorus-bearing blade (*Fig. 1*). The Dent County fronds are similar to this, although several immature plants have small blades with shallowly or deeply notched, rounded tips, rather than attenuate tips. Another frond is forked 3 cm above the base of the blade, and is immature, lacking sori (*Fig. 2*).

Because only a single forked frond is present on most plants, it is unlikely that forking is genetically controlled. Trauma to the tips of young fronds, probably by insects, seems to be the most likely cause, but against this is the Maupin specimen in which the forking occurs at the upper end of the stipe, rather than in the blade itself. Studies are underway to determine the influence of blade-tip trauma on the development of immature fronds. The discovery of forked *A. rhizophyllum* fronds in distinctly different habitats and localities makes it quite likely that forking is of more than occasional occurrence. I suspect that close observation would reveal more plants with forked fronds, which are almost impossible to see at a glance and often require several minutes of search, even when one knows the exact area to be searched.—*James S. Key, Department of Life Sciences, Southwest Missouri State University, Springfield, MO 65802.*

A NOTE ON THE YOUNG FRONDS OF OPHIOGLOSSUM PALMATUM.—In his excellent account of the natural history of *Ophioglossum palmatum* L. in South Florida, Mesler (Amer. Fern J. **65:** 33–39. 1974) writes: "The leaves of *O. palmatum* have been described as palmately or dichotomously lobed, but no ontogenetic evidence has been presented to support either view". I presume he refers to the vernating leaves, as adult forms are obviously lobed and often dichotomous in segmentation. I have grown several plants of *O. palmatum* collected by Wagner and Gómez in 1971 north of San José near Vara Blanca, Province of Heredia, Costa Rica, and have been able to observe the emergence of several generations of fronds under greenhouse conditions. The leaves emerge and uncurl (they are not, like the rest of the Ophioglossaceae, circinnate, but erupt from the substratum almost always bent) and are dichotomously bilobed. Sometimes, they are spathulate, with a rather truncate apex. The laminae are pinkish green, soft but already fleshy, small and quite out of proportion to the petiole, which is many times longer and robust. My specimens, after removal from the original habitat, were planted in well-drained pots, placed under 50% sunlight and at about 75% relative humidity, with temperatures that averaged 18°C. The fronds were able to grow laxly erect. I agree with Mesler that the establishment of subspecies or varieties based on blade morphology and size is not only inconvenient, but, I think, quite improper. The variation in leaf size, shape, texture, and insertion of the sporophylls on the petioles and laminae, is tremendous.—*Luis Diego Gómez P., Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

THE IDENTITY OF POLYPODIUM FURFURACEUM F. PINNATISECTUM.—From 1908 to 1910, Alexander Curt Brade and his brother Alfred collected ferns in Costa Rica. On April 10, 1908 they visited La Carpintera, a series of hills between the cities of San José and Cartago. There they gathered, among other things, a specimen determined by A. C. Brade as *Polypodium furfuraceum* Schlecht. & Cham. that was unusual in having 16–21 lower pairs of pinnae pinnatisect, rather than entire, as is usual in *P. furfuraceum*.

Many years later A. C. Brade described this peculiar plant as *P. furfuraceum* f. *pinnatisectum:* "Differt a forma typica pinnis ex parte pinnatisectis; pinnis 12–16 infimis pinnatisectis, utrinque cum 3–7 segmentis; segmentae usque ad 7 mm longae." The type specimen label also reads in Brade's hand "(? P. lindenianum Kze.)," the name of yet another *Polypodium* with pinnatisect fronds. However, Brade's specimen is in fact the natural hybrid *P. friedrichsthalianum* Kunze × *furfuraceum*. Both parents are very common in the type locality and vicinity, where natural hybrid, *P.* × *aspidiolepis* Baker (*P. friedrichsthalianum* × *thyssanolepis* A. Braun), also occurs. The discovery of the hybrid nature of Brade's plant requires a change in its nomenclatural status:

Polypodium × pinnatisectum (Brade) L. D. Gómez, comb. nov.

Polypodium furfuraceum f. *pinnatisectum* Brade, Bradea 1: 16, *f. 5.* 1969, as "*pinnatisecta.*" TYPE: La Carpintera, Pcia. Cartago, Costa Rica, 1800 m, 10 Apr 1908, *A. & A. C. Brade 16* (HB not seen).

In addition, I have seen one other specimen: Monte de la Cruz, Pcia. Heredia, Costa Rica, 1800 m, *A. Jiménez 208 pro parte* (CR 37368). In view of the apparent facility with which *P. friedrichsthalianum* hybridizes with other species of *Polypodium*, it seems necessary to determine whether *P. lindenianum* Kunze might also be a hybrid involving *P. friedrichsthalianum*.— *Luis D. Gómez P., Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

REVIEWS

COMMON FERNS OF LUQUILLO FOREST, PUERTO RICO," by Angela Kay Kepler, 1975. Spanish and English editions published by Inter American University Press, P.O. Box 1298, Hato Rey, PR 00919. $5.00 paperback, $15.00 hardcover.—Designed as a popular reference, this book covers most of the ferns likely to be found by those who hike the trails of Luquillo Forest and should be a useful field guide to them. Although the 8½ by 11 inch size is not convenient for carrying into the field, the book is useful for quick identifications of ferns because each is illustrated and described clearly. There are keys utilizing soral characters and leaf shapes and a complete list of the ferns and fern-allies in the Luquillo Forest by the author and R. Woodbury. The explanation of terms and general introduction to ferns should be useful to those unfamiliar with ferns who wish to use the book.

Some aspects of the book are annoying to serious students of ferns. The author uses the unnecessary, rather amateurish terms fruitdot and fruitcover to refer to the sorus and indusium, in the descriptions the term ecology is used when habitat is meant, the illustrations are more artistic than scientific (although diagnostic, nonetheless), no index to species or genera is included, and the plants are listed in the distribution list by common names so that someone unfamiliar with the common names adopted or invented by the author is at a disadvantage is finding plants quickly. Some statements (such as the ferns are not differentiated into species as juveniles) have to be reinterpreted by the reader (meaning one cannot identify juveniles to species). The scientific names are based on W. R. Maxon's classification in "Scientific Survey of Porto Rico and the Virgin Islands" (1926) and are somewhat outdated, but are useful in further checking with Maxon's book.

The book includes a map of trails in the forest and a distribution list of the ferns and fern allies to be found along the trails. Considering the book as a whole, it should prove valuable to all visitors to Luquillo Forest and to pteridologists who wish to make convenient identifications of the common pteridophytes of that area.—*J. E. Skog, Department of Biology, George Mason University, Fairfax, VA 22030.*

"TRICHOMANES," Philip. J. Sci. **51**: 119-280, pl. 1-61. 1933; **"HYMENOPHYLLUM,"** Philip. J. Sci. **64:** 1-188, pl. 1-89. 1937; **"GENERA HYMENOPHYLLACEARUM,"** Philip. J. Sci. **67:** 1-110, pl. 1-11. 1938, by E. B. Copeland, reprinted 1975 in one volume by Otto Koeltz, P. O. Box 129, D-624 Koenigstein, W. Germany. DM200.—Of the major botanical monographs published in the pre-World War II Philippine Journal of Science, only two have not been or are not about to be superceded. The 1930's depression which reduced subscription sales, and the War in which all back issues were destroyed, combined to make their reprinting a necessity. Otto Koeltz has obliged with both Bartram's 1939 "Mosses of the Philippines" and Copeland's three-part study of the Hymenophyllaceae.

Copeland's trilogy is close to his final word on the subject. "Trichomanes" (1933) dealt with 113 Old World species including *Cardiomanes*, and "Hymenophyllum" (1937) with 127 species; "Genera Hymenophyllacearum" (1938) apportioned these and many New World species into 33 genera with the contention that the two customary ones were polyphyletic. To these, Copeland added only a short paper with notes and novelties from New Guinea (Philip. J. Sci. **73**: 457-469, pl. 1-4. 1941), a 34th genus based on a New Caledonian oddity (Gen. Fil. 36. 1947), a treatment of the Philippine species (Fern Fl. Philip. **1**: 46-82. 1958), and minor scattered miscellany.

Thus, since 1938 botanists have been able to choose from two generic treatments, both presented by a single author: a Hymenophyllaceae either with over 30 genera, or with 2 main genera plus one to several isolated minigenera.

While Copeland's taxonomy and nomenclature are subject to considerable revision, of major lasting value in his work are the numerous magnificent detailed illustrations. "Hymenophyllum" and "Genera Hymenophyllacearum" were

illustrated by the two Filipino artists, Leopoldo A. Alicbusan and Esteban P. Borbe, who worked with Copeland for 14 months in his private herbarium then located at Los Baños, Laguna, Luzon. The microscopic details were drawn with camera lucida from slides prepared by Copeland. Mr. Borbe has told me that Copeland demanded precise reproduction without stylizing, and eventually came to trust the skills of his artists so completely that he did not always compare the completed drawings with the specimens. Each drawing was made on separate paper; the final lay-out of the plates was Copeland's. Alicbusan survived the infamous "Death March" upon the fall of Bataan in 1942, and after the War made a career in the military, meeting a soldier's death in 1954. Borbe is still working from retirement as an artist.

The reprint is handsomely bound with good quality paper. The single volume is one-half the weight and thickness of the three originals if separately bound. Page size is reduced, but only by the eliminating of the unnecessarily large margins. Unlike those in the original, the plates are on both sides of the pages; reproduction is good. The single and very serious fault is the lack of an index. Each volume of the Philippine Journal of Science proper has an index although not including the plates (and plates are not referenced back to the text). The inexcusable failure to make an index to the reprint will waste a great deal of time for users.

Copeland's work on Hymenophyllaceae deals hardly at all with the three European species or the ten temperate North American species. But it is absolutely indispensable for those with a broader interest in this principally tropical and south temperate family. And as the first modern effort to make sense out of the filmy ferns, it provides an overall perspective that is the requisite foundation for further work.—*M. G. Price, University of the Philippines at Los Baños, College, Laguna 3720, Philippines.*

"ENUMERATIO PTERIDOPHYTARUM JAPONICARUM, FILICALES" by Toshiyuki Nakaike. xii + 375 pp. 1975. University of Tokyo Press, 7-3-1 Hongo, Bunkyo-ku, Tokyo, 113-91, Japan. Distributed in the U.S. and Canada by International Scholarly Book Services, P.O. Box 4347, Portland, OR 97208. $29.50/ £ 12.90/8,000 yen.—This is a disappointing book, mostly because of what is not included. It is basically what the title states: an enumeration of Japanese Filicales, some 800 taxa. There are no keys, no descriptions, no discussions, no illustrations, and, except of genera, no citation of types. We are given the accepted name, homotypic and heterotypic synonyms, and chresonyms [a useful term for *sensu* names coined by H. M. and Rozella B. Smith (Syst. Zool. **21:** 445. 1972)], all with exhaustive literature citations to floras, checklists, and other taxonomic notes that indicate how these taxa have been treated historically. In addition, there is a brief statement of distribution and the Japanese common name. Essentially, then, we have one man's statement at a point in time with regard to the classification of Japanese ferns—the author's stated objective. The effort involved in compiling the synonymy and references was no doubt staggering. For me, though, a classification presented in this manner does nothing to provoke or promote additional research. It implies something immutable about taxonomy,

when in fact it is likely that this classification will be supplanted by a new one in a few years.

There are over 75 "new combinations" in the book, many of them involving the impermissible taxonomic category "monstrosity." Nakaike elevates two infrageneric names to generic rank, *Lacosteopsis* and *Nothoperanema*. However, the latter generic name, as well as two species combinations made by Nakaike (*N. hendersonii* and *N. shikokiana*), should be attributed to Ching (Acta Phytotax. Sin. **11:** 25. 1966).—*Alan R. Smith, Herbarium, Department of Botany, University of California, Berkeley, CA 94720.*

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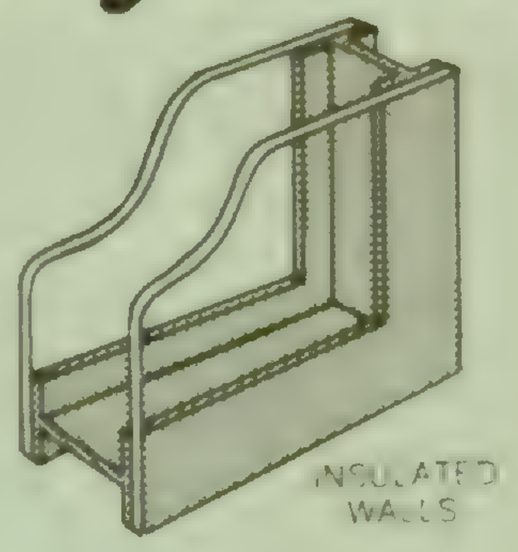

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AMERICAN FERN JOURNAL

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Edgar Wherry in Pennsylvania

JOHN M. FOGG, JR.*

Edgar Theodore Wherry was born in Philadelphia on September 10, 1885, and received his education at Friends Central School and the University of Pennsylvania. After teaching at Lehigh University from 1908 to 1913 and working in Washington, D.C. for seventeen years, he returned in 1930 to the city of his birth and has resided there ever since.

Long before he returned to Philadelphia to live, local botanists became acquainted with Dr. Wherry. Since his family resided in this city, it was his habit to spend the Christmas holidays with them. This led to his being invited to speak at the December meeting of the Philadelphia Botanical Club, an organization which had been founded in 1891.

The earliest of his lectures which I can remember was in 1921, when his topic was "Our Native Plants and their Soil Preferences." From that time on for many years, with only a few exceptions, his December presentation was an annual feature of the Club's programs, and we were favored with lectures on ferns, orchids, pitcher plants, heaths and heathers, and of course, *Phlox* at the time when our speaker was preparing his monograph on that genus. All of his talks were illustrated with handcolored slides.

In 1930 Dr. Wherry joined the faculty of the Department of Botany of the University of Pennsylvania, where he taught until his retirement in 1955. He had already made substantial contributions to our knowledge of soils, had perfected a colorimetric method for determining soil pH, had investigated the remarkable stand of box huckleberry (*Gaylussacia brachycera*) in Perry County, Pa., and had published an account of the "Wild Flowers of Mount Desert Island, Maine."

In 1918, while still employed by the Bureau of Chemistry in the U.S. Department of Agriculture, Wherry became a member of the American Fern Society. He was president of that organization from 1934 through 1938 and was the author of many articles in the "American Fern Journal." He assigned the royalties from his popular "Fern Guide" to the Society. This is entirely typical of the selflessness of the man. Today he is deservedly an Honorary Member of the Society.

In 1932 the University of Pennsylvania inherited the property which became the Morris Arboretum. Dr. Rodney H. True, who was then Chairman of the Department of Botany, assigned four members of his staff on a part-time basis to administer the project, and Wherry was appointed ecologist. One of his first tasks was to conduct a detailed soil survey of the grounds. This revealed that within some 175 acres there was a wide diversity of soil types. The ridge which traverses the property from east to west is composed of quartzite which, being a metamorphosed sandstone, weathers slowly to produce an acid soil. On the south slope this gives way to circum-neutral soils derived from schistose rocks, while northward the underlying formation is Cambro-Ordovician limestone, a distinctly alkaline soil. With this information in hand, it was possible to develop planting

*Arboretum of the Barnes Foundation, Merion, PA 19066.
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plans in a scientific manner, making certain that each family or genus was established on soils with which it was compatible.

In 1934 the Bowman's Hill State Wild Preserve was established with the aid of the Works Progress Administration. This preserve, which is located near New Hope in Bucks County, Pa., is dedicated to the growing and preservation of plants native to the Commonwealth. With Wherry's deep-seated interest in wild flowers it was inevitable that he should be attracted to this project, and in 1935 he became one of the Founders. For a time he was Chairman of the Preserve and has been one of its botanical advisors for 41 years. The Wherry Fern Trail was one of the first trails to be developed at the Preserve and appropriately commemorates Dr. Wherry's dedication to that group of plants.

In the mid 1930's, work was begun in earnest on a state Flora at the University of Pennsylvania. The Department of Botany had purchased a twenty-passenger bus to transport students between the campus and the arboretum, and each spring, as soon as classes were over, we rounded up half a dozen or so of our abler students, loaded up the bus with presses, driers, and collecting papers, and set off on a week's botanizing trip. During several summers we moved from east to west across the northern tier of Pennsylvania counties, combing every available habitat. We hoped eventually to cover the entire state. Frequently we returned to the area later in the season to collect fruiting material. From each of these trips thousands of herbarium specimens were brought back to be incorporated into our records and finally to appear as dots on our outline maps of the state. Edgar Wherry participated in many of these trips, and his knowledge of geology, geography, and the more interesting wild flowers made him a valuable member of the party.

Enthusiastic field man that he was (and at the age of 90-plus still is), he always welcomed the prospect of a collecting expedition. I recall with much pleasure a foray on which I accompanied him across Pennsylvania in the fall of 1940. We drove through Cameron, Elk, Jefferson, and Armstrong counties, stopping frequently to collect. After visiting the extreme southwestern corner of the state, we came back through Fayette County, stopping near Elliottsville to collect *Clethra acuminata* at what was then its only known station in Pennsylvania. We could almost look across the state line into Maryland, but there was no doubt about it—the *Clethra* was definitely in Pennsylvania, although it is not so recognized in the eighth edition of "Gray's Manual."

Next we visited Ohiopyle, in the same county, where several genera such as *Boykinia* and *Marshallia* are at or near the northern limits of their range. Continuing eastward, we stopped at a locality southwest of Reels Corners to collect that unique sedge *Cymophyllus fraseri* at one of its few known stations in the state. Each of us brought back from this brief trip about 400 numbers (many of them in replicate), which added a significant number of records to our study.

On another occasion a friend of mine offered us the use of his hunting lodge near Bradford in McKean County in the extreme northern portion of the state. My wife and I, accompanied by Wherry and Joseph W. Adams, who was then on the staff of the Morris Arboretum, spent five days in a lovely spot scouring the coun-

tryside, with the result that we brought back nearly a thousand numbers from an area that was almost entirely unknown botanically. I mention these two trips merely as an indication of Edgar Wherry's active interest in the Flora project and his willingness to drop anything he might be doing in order to participate in the field work.

In 1941 I accepted an appointment as Dean of the College of Arts and Sciences at the University, having been assured that my duties would not seriously affect my work on the Flora. Of course, no one at that time knew that soon the country would be at war and that afterward there would be a lengthy period of readjustment affecting all educational institutions. The result was that for twelve years I was able to devote very little time to the project. It might have been necessary to abandon it altogether, had not Wherry stepped in and assumed the responsibility for continuing it.

Fortunately, also, at this juncture I was able to enlist the cooperation of my friend and colleague, Dr. Herbert A. Wahl, Professor of Botany at Pennsylvania State University. On three separate occasions during my involvement in administrative duties, Herb was able to obtain a year's leave of absence from Penn State and to come to Philadelphia to work with Wherry on the Flora. I joined them whenever possible, but my appearances were few and far between.

The various techniques adopted for handling our multitudinous records have been described in detail elsewhere, and need be mentioned only briefly here. Most of them were devised by the late Dr. J. R. Schramm, formerly Chairman of the Department of Botany, to whom tremendous credit is due for his support of the Flora project.

Once the thousands of specimens of Pennsylvania plants we collected had been mounted, it was necessary for their identifications to be authenticated before they were ready to be recorded and mapped. In this operation Dr. Wherry assumed responsibility for such groups as the pteridophytes, orchids, Ericaceae, Polemoniaceae, and a few others. Herb Wahl, a recognized authority on *Carex* (our state's largest genus), worked with the entire Cyperaceae, as well as the very difficult genus *Potamogeton* and many of the apopetalous families. I took over *Juncus* and most of the Sympetalae, and in this manner there gradually evolved a division of labor, with Wherry taking more and more groups as time went by and my association with the project decreased.

After the name on a given specimen was authenticated, it was entered on a master record card that listed the state's 67 counties. The exact locality at which each specimen was collected was then entered, in carbon-base ink, under its appropriate county, together with name of the collector, his number or date of collection, and a symbol indicating the herbarium in which the sheet had been examined. The last was thought to be of value since, in addition to incorporating about 100,000 specimens in our own herbarium, we attempted to record all of the Pennsylvania material in the Philadelphia Academy of Natural Sciences, the Carnegie Museum in Pittsburgh, the State Museum in Harrisburg, and the herbarium at Pennsylvania State University. Probably no other state Flora has ever been based on such a tremendous number of specimens.

The final step in the procedure was to place on an outline map of the state for each species a dot representing each entry on the record cards. Accuracy is of great importance because the state includes diverse physiographic provinces, such as the coastal plain, the piedmont, the valley and ridge province, and the Appalachian plateau. The state is also traversed by the terminal moraines of two recent glaciations. From almost the very beginning of the undertaking this has been Edgar Wherry's sole responsibility. There is probably not a town, village, or hamlet in the Commonwealth of Pennsylvania for which he does not know the exact location. Needless to say, we have disregarded all specimens with vague data and have recorded only those giving precise information.

Of the more than 3000 species of higher plants which occur in Pennsylvania, about 800 are introduced, either from abroad or from other sections of the United States. Of those which are native, the majority are widespread, occurring in every or almost every county (*Fig. 1*). Others have a more limited distribution, being either predominantly northern, or southern, or on the coastal plain, or components of the Ohio River vegetation. Still others might be found only on particular soils, such as limestone (*Fig. 2*), serpentine, or shale barrens. As Wherry's carefully placed dots began to fill in the map-cards, often several hundred for each species, these correlations became abundantly evident.

Another fact which emerged was that in countless instances species were totally lacking from counties where they might be expected to be common. Wherry then began making "Wanted Lists" for each county. If he knew of an active collector in one of these counties, he would send him a list and urge him to collect. More often than not he would execute this commission himself, spending days in a given county to collect the plants which had been neglected by other botanists. Usually these were common plants, for all too frequently rare or spectacular species are collected at the expense of more familiar ones.

Another by-product of the maps is species lists for given counties, which Wherry has compiled. Several lists have already been published in "Bartonia," the official journal of the Philadelphia Botanical Club. They are the basic bricks of which state and regional Floras are constructed.

It was the original intention that the Flora of Pennsylvania should be biologically oriented and contain diagnostic keys, brief descriptions, and interpretive information concerning distribution, which would elevate it above the level of a mere checklist. To that end, Edgar Wherry, Herb Wahl, and I prepared hundreds of pages of manuscript. Unfortunately, Wahl's increasing preoccupation in monographing *Chenopodium*, his recent untimely death, and my increasing involvement in administrative duties reduced this objective to a rather forlorn hope. Also, the cost of publishing such a work, plus our many hundreds of range maps, would have been almost prohibitive.

It is a pleasure, however, to report that our manuscript, incomplete though it is, has been turned over to Dr. Carl Keener of the Department of Botany at Pennsylvania State University. Carl feels that is may be possible to put it in shape for publication, and if he does, Wherry's treatments of the ferns, orchids, phlox, etc. will constitute a substantial contribution.

As matters stand at present, only the maps, in the form of an "Atlas," are scheduled for publication at an early date. It is unlikely that anyone examining these maps will gain any real insight into the forty years of field work and herbarium study which underly them, but I hope it has been made clear that to a large degree their publication is due to the indomitable energy of one very versatile and energetic individual.

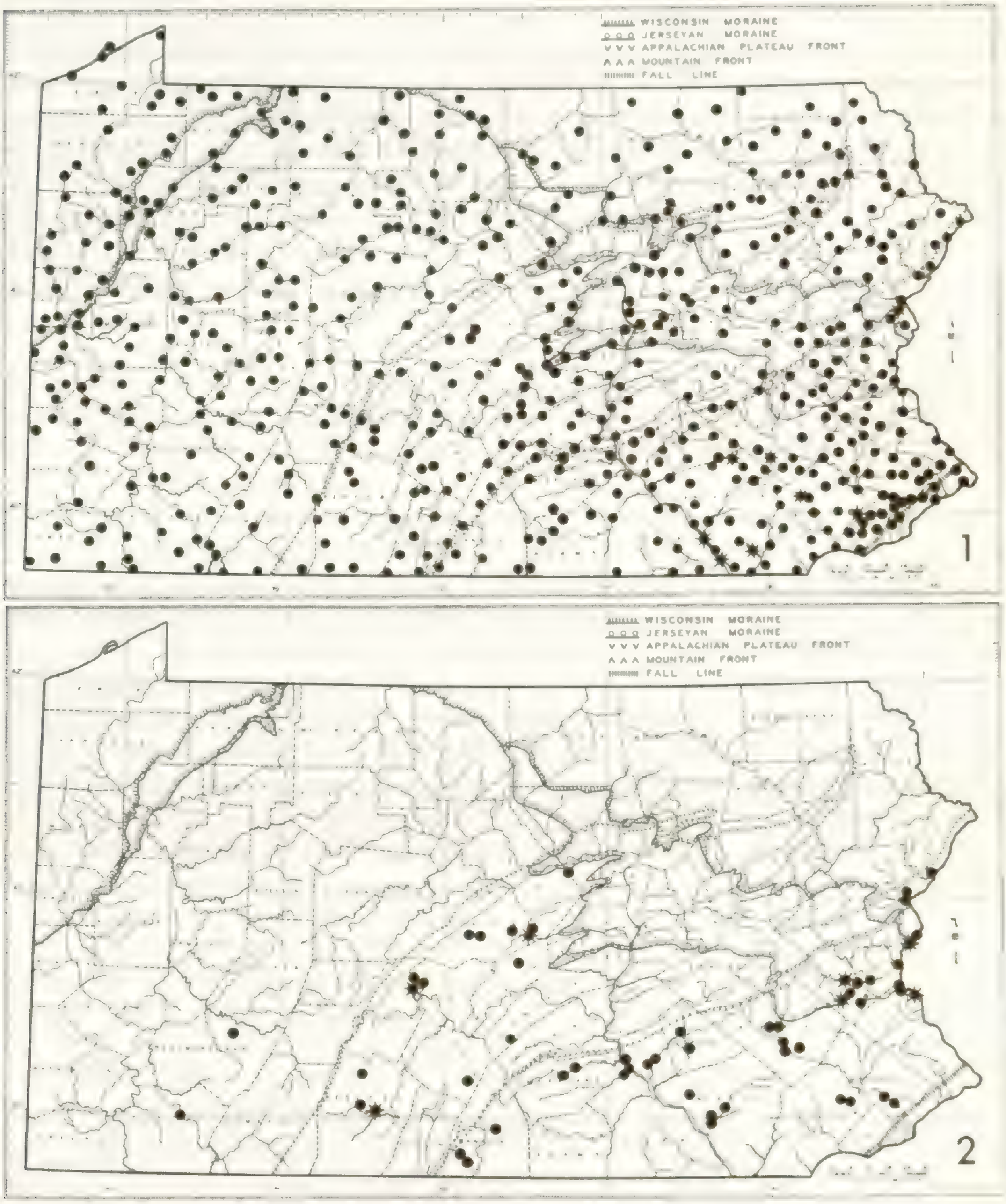

FIG. 1. Pennsylvania range of *Polystichum acrostichoides*. FIG. 2. Pennsylvania range of *Asplenium cryptolepis*.

In the meantime, from 1941 to 1950 and again from 1953 to 1957, Dr. Wherry served as a member of the faculty of the School of Botany, Horticulture and Landscape Architecture of the Arboretum of the Barnes Foundation. This school had been established in 1940 by Mrs. Laura L. Barnes, Director of the Arboretum, and the courses offered at her invitation by Wherry during these two intervals included geology, soils, ecology, and plant physiology. His emphasis at all times was on the out-of-doors, where the study of botany truly belongs.

In 1972 the officers of the Delaware Valley Chapter of the American Rock Garden Society approached the Barnes Arboretum with a proposal to establish a small rock garden in honor of Dr. Wherry. He had been editor of their quarterly publication for several years and is today Editor Emeritus. The chapter proposed to construct this garden if the arboretum would provide space for it. Today there exists on a south-facing slope a plot 75 × 10 feet named the Edgar T. Wherry Memorial Garden. In this garden grow only plants which Wherry himself has selected. They are either species which have been named for him (such as *Silene wherryi* and *Tiarella wherryi*) or those with which he has had some intimate association, either as discoverer, introducer into cultivation, or author, as in several species of *Phlox*.

Another interesting feature of this garden is its ecological character. The soil at the western end is derived from sandstone and is therefore acid. This is followed by a section of flaky shale, which produces a neutral reaction. The eastern end is rendered circum-neutral by the addition of limestone chips. Needless to say, this dramatic demonstration of the correlation between plant species and soil types is of considerable interest to both students and visitors to the arboretum.

At least one day a week throughout the growing season, Edgar Wherry may be found in his garden, weeding, mapping, or planting specimens which have been sent to him by friends from many sections of the country.

Mrs. Barnes had always been interested in hardy ferns, and in the two acres of native woodland which occupy the southwestern corner of the arboretum had assembled a collection of about a hundred species, including some rather rare and interesting exotics, such as *Dryopteris erythrosora*, *Arachniodes standishii* and *Osmunda japonica*.

During the summer of 1975 Dr. Wherry suggested that a fern trail be established in these woods in honor of Mrs. Barnes. He personally checked the identifications of all of the species, new plastic labels giving the botanical and common names were made, directional arrows were installed, and the Laura L. Barnes Fern Dell became a reality. It has already been visited by the newly formed Delaware Valley Fern Society, of which Edgar Wherry is an honored member, and we are confident that it will prove a valuable teaching adjunct as well as a feature of interest to others who visit the arboretum.

Botanists here and elsewhere—especially members of the American Fern Society—may well be grateful for the "return of the native" to the state and city of his birth.

Perry Creek, Washington, a Fern-watcher's Eldorado

A. R. KRUCKEBERG*,[1]

The vascular plant flora in the major drainage systems of western Washington is highly predictable from one river valley to the next. The typical coniferous forest plants reoccur throughout the region. This expectation holds as well for the ferns and fern-allies in the cismontane Pacific Northwest. The same species, Bracken (*Pteridium aquilinum* var. *pubescens*), Sword Fern (*Polystichum munitum*), Lady Fern (*Athyrium filix-femina*), Oak Fern (*Gymnocarpium dryopteris*), and Deer Fern (*Blechnum spicant*), can be expected in the usual range of forest communities. But the botanist-naturalist is in for a big surprise along a two-mile segment of the Perry Creek trail in Snohomish County, Washington, about 40 miles northwest of Seattle. No fewer than 26 species of ferns and fern-allies are known from this remarkable locality. It is a truly exceptional habitat well within the lowland coniferous forest biome.

The first detailed collecting in Perry Creek was that of Mr. John W. Thompson in the 1930's. Thompson, then a high school biology teacher in Seattle, had a keen eye for the unusual. His collections of Pacific Northwest plants turned up many a novelty. A complete set of his collections was acquired by the University of Washington Herbarium, where Thompson served as assistant curator from 1943 to 1960.

Following Thompson's discovery of the diverse ferns of Perry Creek, the locality has been visited frequently by botanists and amateur naturalists. In 1963, Dr. Warren H. Wagner, Jr. visited Perry Creek in the company of the author. Wagner's interest in the locality was whetted by the earlier Thompson finds—seven species of *Botrychium* and the sympatric occurrence of three *Polystichum* species. It was on this foray that Wagner found the hybrid between *P. andersonii* and *P. munitum* (Wagner, 1973). The richness of the Perry Creek fern flora was revealed to other pteridologists in 1969. A trip to the area, led by Drs. Wagner and T. M. C. Taylor, was made during the 12th International Botanical Congress, held that year in Seattle. Members of the foray were able to verify the occurrence of many pteridophytes that Thompson had first found.

PERRY CREEK FERNS

The following paragraphs list the pteridophytes that occur along the first two miles of the Perry Creek Trail. This listing is compiled from observations and herbarium records (WTU) made over the years. The most recent corroboration of this list was made on September 11, 1975 by members of the Fern Study Group of the Northwest Ornamental Horticultural Society and the author.

Although most of species listed are frequent to common in western Washington, it is exceptional to find them so closely associated in a single, rather small natural area. The occurrence of *Polystichum andersonii*, its hybrid with *P. munitum*, *P.*

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[1] I am indebted to W. H. Wagner, Jr. and T. M. C. Taylor for their valued counsel over the years on the ferns of Perry Creek. Two members of the Fern Study Group (Northwest Ornamental Horticultural Society), Mareen S. Kruckeberg and Sue Olsen, have been helpful in the field surveys. Thanks are due David Wagner for data from this recent forays in the area.

lonchitis, Asplenium trichomanes, Dryopteris filix-mas, Cryptogramma crispa, three *Lycopodium* species, and seven *Botrychium* species are of special interest.

Adiantum pedatum L. is frequent and often gregarious on lush, shady talus under hardwoods.

Asplenium trichomanes L., so common along the Perry Creek Trail on wet talus mostly under hardwoods, is infrequent and local elsewhere. At Perry Creek it is nearly as abundant as *Cryptogramma crispa,* a fern found everywhere on the more open but moist talus.

Athyrium filix-femina (L.) Roth is very common throughout the area; in forb-rich talus habitats it is the dominant forb.

Blechnum spicant (L.) J. Smith is restricted to regenerating, clear-cut Hemlock-Fir forest near the trail head and is rare on wet talus.

Botrychium boreale Milde, *B. dusenii* (Christ) Alston, *B. lanceolatum* (Gmel.) Ångst., *B. lunaria* var. *onondagense* (Underw.) House, *B. multifidum* (Gmel.) Trev., *B. simplex* E. Hitchc., and *B. virginianum* (L.) Swartz are all infrequent on wet, mossy talus in hardwood glades. None is at all common, although *B. multifidum* is not infrequently encountered from the coast of Washington up to mid-montane altitudes. Some years it has not been possible to locate the other species, even after intensive searches above and below the trail. It was considered the high point of the 1969 pre-Congress foray for the party to have rediscovered all of the Grape Fern species located many years before by Thompson.

Cryptogramma crispa (L.) R. Br. is common on wet talus, with or without hardwood cover. The plants are unusually large and lush, and well below their usual lower altitudinal limit. In the Cascade and Olympic Mountains, *C. crispa* normally occurs on subalpine talus and rock outcrops.

Cystopteris fragilis (L.) Bernh. is rare under the cover of hardwoods on talus.

Dryopteris filix-mas (L.) Schott is another fern of sporadic and infrequent occurrence in the west (Reisender, 1974), and is not common at Perry Creek, having been collected by Mickel in 1969 and Denton in 1974. It was from a plant collected at Perry Creek (Snohomish, not Chelan County) that Reisender obtained the first chromosome count ($2n=82$, tetraploid) of any western member of the complex.

Dryopteris assimilis S. Walker (=*D. austriaca* (Jacq.) Woynar) is infrequent, mostly in coniferous woods.

Gymnocarpium dryopteris (L.) Newm. is occasional but gregarious in coniferous woods and under hardwoods on talus.

Lycopodium clavatum L. is infrequent in regenerating, clear-cut forests, with Deer Fern. *Lycopodium miyoshianum* Makino is present at Perry Creek, according to Mr. Joseph Beitel (pers. comm.). It occurs on wet, moss-covered talus in the shade of Vine Maples. *Lycopodium selago* subsp. *patens* (Beauv.) Calder & Taylor, although frequent at Perry Creek in habitats like those of *L. miyoshianum*, seldom makes more than a sporadic appearance in the Pacific Silver Fir zone elsewhere in our area.

Polypodium glycyrrhiza D. C. Eaton occurs mostly on trunks and limbs of Maples. *Polypodium hesperium* Maxon (or possibly *P. montense* Lang) grows on rocks in crevices, and is infrequent.

Polystichum andersonii Hopkins is frequent under hardwoods on moist talus slopes. It is sporadic and infrequent in the Pacific Northwest; its few localities are widely separated throughout its range from northwestern Oregon to southeastern Alaska and east to Montana. The hybrid of *P. andersonii* with *P. munitum* is sporadic and rare, and usually occurs with both parents. It has been found on Mt. Hood, Oregon, and on Mt. Rainier, Washington, according to David Wagner (pers. comm.). *Polystichum lonchitis* (L.) Roth typically is a fern of high, wooded to open talus in the fringes of the subalpine forest, the Mountain Hemlock Zone of Franklin and Dyrness (1973). The Perry Creek station is certainly the lowest in elevation for this fern in Washington. It is intermittent mostly under hardwoods on talus, but also occurs on open talus slopes. Obvious hybrids involving *P. lonchitis* with *P. munitum* or *P. andersonii* have not been discovered, despite attempts to find them. *Polystichum munitum* (Kaulf.) Presl is locally abundant, elsewhere frequent, mostly in the shade of hardwoods or conifers.

Pteridium aquilinum var. *latiusculum* (Desv.) Underw. is locally abundant, mostly along the Perry Creek trail.

Selaginella wallacei Hieron. is frequent on moss-covered talus boulders, mostly in the open.

VEGETATION OF THE PERRY CREEK AREA

The Perry Creek fern habitat is a most exceptional enclave within the broadly distributed lowland coniferous forest biome (Western Hemlock or *Tsuga heterophylla* Zone of Franklin and Dyrness, 1973) in western Washington. One needs only to traverse similar tributary canyons of the major river systems of the Puget Sound basin to discovery why. Whereas most such drainages are uniformly clothed with a mixed coniferous forest of Douglas Fir, Western Hemlock, and Western Red Cedar, with associated typical understory species, the fernery of Perry Creek is located along a succession of hardwood glades, patches of exceptional assemblages of conifers of smaller than usual stature, and open talus, all on steep, moist slopes. The hardwoods are chiefly maples: *Acer macrophyllum* of low and sparse profile, along with thickets of the shrubby *A. circinatum* and *A. glabrum*. The Maple thickets frequently are replaced by similarly dense stands of deciduous, shrubby *Cornus stolonifera* or pure forb communities dominated by *Athyrium filix-femina* and *Rubus parviflorus*.

Hardwood thickets are the dominant community on wet talus, and contain no conifers. The seed plants and associated ferns are: *Acer circinatum, A. glabrum, *Actaea arguta, Alnus rubra, Aruncus sylvester, Athyrium filix-femina, Carex mertensii, Cornus stolonifera, *Elymus glaucus, Epilobium angustifolium, Geum macrophyllum, Oplopanax horridum, Osmorhiza occidentalis, Pteridium aquilinum* var. *latiusculum, Ribes petiolare, Rubus parviflorus, R. spectabilis, Sambucus racemosa, Sorbus sitchensis, Thalictrum occidentale, *Tolmiea menziesii, Valeriana sitchensis*, and *Veratrum viride*. The species with asterisks apparently are restricted to trailside. It is in the understory of these hardwood glades that most of the Perry Creek ferns occur, although several species extend beyond onto the massive bouldery talus tracks between the hardwood glades.

On slightly less precipitous slopes, one finds open, coniferous woods, but not of the same composition as those of the climax coniferous forests on adjacent slopes. Rather, Alaska Cedar (*Chamaecyparis nootkatensis*), Subalpine Fir (*Abies lasiocarpa*), Douglas Fir (*Pseudotsuga menziesii*), and Western Hemlock (*Tsuga heterophylla*), all of smaller than expected stature, occur interspersed with the same hardwood dominants mentioned above.

Open, bouldery talus has a rich cover of mosses and lichens. The frequent ferns are: *Cryptogramma crispa, Asplenium trichomanes, Lycopodium selago* subsp. *patens*, and *Selaginella wallacei*. Very few angiosperms occur, among them *Montia flagellaris, Saxifraga bronchialis*, and *S. ferruginea*.

Wooded, bouldery talus replaces hardwood thickets or open talus on gentler slopes, and yet has the same rocky nature. This habitat is dominated by Alaska Cedar, although *Acer macrophyllum* also is common. Douglas Fir and Pacific Silver Fir (*Abies amabilis*) are occasional. Thick carpets of moss occur on the shaded talus, commonly with *Asplenium trichomanes, Cryptogramma crispa, Goodyera oblongifolia, Montia flagellaris*, and *Polystichum munitum*.

Nearly everywhere along the two-mile sector of the trail the substrate is rocky, ranging from gravelly textured scree to massive, jagged boulders arranged in long, steep talus slopes. Although the soil is shallow to non-existent, the rock is mantled with a luxuriant coat of mosses and lichens. This non-vascular mat serves as a substrate for the ferns, fern-allies, grasses, forbs, and even for some of the woody plants. In sum, we find a microcosm of wet, rocky talus surrounded by the climatically dominant coniferous forest; the former must be an enclave caused by a unique combination of environmental factors.

In the absence of carefully instrumented monitoring of the habitat, some of the operational factors may be inferred by observing the topography and the biological indicators of the area.

Perry Creek is a tributary of the south fork of the Stillaguamish River in central Snohomish County, western Washington (*Fig. 1*). It is well within the lower to mid-montane transition zone along the western flanks of the Cascade Range. The terrain along this sector of the Stillaguamish drainage is one of spectacularly sheer and high peaks rising abruptly out of the valley floor, which lies at ca. 1700 feet altitude. Perry Creek itself is in a narrow, steep-sided canyon bounded on the east and west by two dominating peaks, Mount Dickerman (5266 feet) and Stillaguamish Peak (5863 feet). Downstream from Perry Creek, just beyond its junction with the Stillaguamish River, is the massive, sheer wall of Big Four Mountain (6120 feet), which has on its north-facing slope permanent snowfields and at its talus base low-lying snowfields that are sculpted into the well known Ice Caves near Big Four. At the Ice Caves, the local environment and flora are truly subalpine, despite the altitude of only 1800 feet.

Given the frigid shelter of towering mountain walls on all sides, the occurrence of a truncated and telescoped sequence of "life-zones" is not unexpected. Under the usual conditions of gradual increase in elevation, the shift from the Western Hemlock through the Pacific Silver Fir to Mountain Hemlock Zone, with their attendant plant communities, would be gradual and not perceptible over short

distances. But at Perry Creek and at other sites along the Stillaguamish River, abrupt topographic and associated local climatic changes cause similarly abrupt changes in the floristic assemblages. But this inference from topography and climate alone does not wholly explain the hardwood scrub and talus communities within the foreshortened zonation of coniferous forest life-zones. I believe it is a matter of two integrated physical factors. First is the local climate, which provides a cool, moist habitat, shaded for much of the day. Second is the unstable, boulderly talus. Both climate and substrate provide niches for ferns and other plants from diverse communities. Further, the talus of the hardwood glades that contain the bulk of the fern species is rich with mosses, which provide an optimally moist substrate for ferns throughout their life-cycles.

FIG. 1. Looking down Perry Creek to the canyon of the south fork of the Stillaguamish River and Big Four Mountain on the horizon. Photo courtesy Mr. J. W. Thompson.

The nearest weather station to Perry Creek is at Silverton (1500 feet), about 5 miles west and downstream in the same river valley. From weather records (*Table 1*) it is easy to see that winter temperatures decrease and precipitation increases across the altitudinal transect from Puget Sound to the lower montane elevation of the Stillaguamish River. Undoubtedly, winter temperatures are still lower and precipitation greater along Perry Creek.

The Washington State geological map (Huntting, 1961) portrays the rocks in the region of Perry Creek as pre-Jurassic sediments. It has not been possible to identify the particular sedimentary rocks along the crucial stretch of wet talus that

supports the ferns. The entire formation is complex, and according to Huntting (1961), consists of "graywacke, argillite and siltstone with some slate and phyllite; [it] includes graywacke breccia and ribbon chert with minor local limestone lenses and basalt flows."

The entire drainage of the south fork Stillaguamish River is exceedingly rich floristically and includes other fern species besides those that cluster along the Perry Creek talus. From herbarium records and observations by the author, the following ten pteridophytes can be added to the Perry Creek list. Three species characteristic of ultramafic (high magnesium) rocks occur in the nearby upper Coal Creek drainage: *Aspidotis densa* (Brack. in Wilkes) Lellinger, *Adiantum pedatum* subsp. *aleuticum* (Rupr.) Calder & Taylor, and *Polystichum mohrioides* var. *lemmonii* (Underw.) Fern. (Kruckeberg 1969, p. 84). David Wagner (pers. comm.) confirms the presence of *Polystichum kruckebergii* Wagner along with *P. mohrioides* var. *lemmonii* on Devil's Thumb, also in the upper Coal Creek drain-

TABLE 1. CLIMATIC DATA FOR PORTIONS OF SNOHOMISH COUNTY, WASHINGTON[1]

Station and altitude	*Distance* (mi) *from Perry Creek*	*Temperatures* (°F) *Jan. average*	*July average*	*max.*	*min.*	*Precipitation* (in) *Annual average*
Everett, 100 ft	40	38.0	61.2	99	3	32.74
Granite, Falls 391 ft	20	—	—	—	—	59.41
Silverton, 1500 ft	5	33.0	61.2	103	0	94.80

[1]Data from U.S. Dept. of Agriculture (1941, p. 1173).

age, as reported first by Slater (1967). D. Wagner also found *Lycopodium sitchense* Rupr. in the same area. *Athyrium distentifolium* is a common talus species in the subalpine sections of the drainage; it is also at the Ice Caves. Other ferns and fern-allies known to occur in the Perry Creek drainage basin are *Asplenium viride* Huds. (Mt. Dickerman), *Thelypteris limbosperma* (All.) H. P. Fuchs (Monte Cristo), *T. phegopteris* (L.) Slossen (Big Four Mtn.), and *Woodsia scopulina* D. C. Eaton (Mt. Dickerman). Expected, but not yet found, in the Stillaguamish River drainage are *Cheilanthes gracillima* D. C. Eaton, *Cryptogramma stelleri* (Gmel.) Prantl, *Dryopteris arguta* (Kaulf.) Watt, *Pityrogramma triangularis* (Kaulf.) Maxon, *Selaginella oregana* D. C. Eaton in Wats., and *Equisetum* spp.

The Perry Creek fernery is within the jurisdiction of the U.S. Forest Service (Monte Cristo Ranger District, Snoqualmie-Mt. Baker National Forest). Although there seems to be no immediate danger to the habitat, it is conceivable that mining or logging operations in other parts of the Perry Creek drainage could pose a threat. When I first visited the site in the early 1950s, our party hiked in from the bottom of the river valley through a virgin Hemlock-Cedar-Douglas Fir forest before reaching the fern-hardwood talus. The lower coniferous forest was logged in the late 1950's to within ¼ mile of the critical fern habitat. It is to be hoped that

the Forest Service will take steps to preserve the Perry Creek fern area in perpetuity, either as a Botanical Area or as a Research Natural Area. At present the trail through the site is a tolerable and handy intrusion, but no further modification of this priceless botanical and scenic habitat should occur.

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Origin of the Pteridophyte Flora of The Bahamas, Caicos and Turks Islands

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The region under consideration might be likened to the open mouth of a vast sack of tropical and subtropical plants of all categories. It is a region, excluding Bermuda, that is occupied by the farthest northeastward extension of floristic elements which have their optimum development to the south (in Cuba, Hispaniola, and Puerto Rico) and west (in Florida). Subtropical southern Florida and its keys also have been recipients of the Greater Antilles flora.

According to the best authorities, the geological processes of emergence and subsidence have affected the low-lying Bahamas more than once in the past. During periods of greatest emergence, the islands of the relatively shallow Little Bahama Bank (primarily Grand Bahama and Abaco) were connected. The same is true of the islands of the Great Bahama Bank (primarily New Providence, Eleuthera, Cat, Exuma, Long and Andros). However, the great depth of water between the two banks has precluded their ever having been connected. All of the islands scattered to the south of the Great Bahama Bank also have such depths of water between them that apparently they have never been connected; the main islands in this group are San Salvador, Crooked, Acklin, Mariguana, Inagua, Caicos and Turks. Finally, the great depth of water between all of the above islands and Florida, Cuba, and Hispaniola would appear to have prevented their ever having been connected, except for a possible connection of Great Bahama Bank with Cuba during the last Ice Age, about 25,000 years ago. That connection would account for some of the animal life now known to occur on some islands in this region. The dissemination of plants into the islands from the south and west has had to rely entirely upon agencies other than overland migration, since such routes apparently have never existed.

Although there are several factors that affect the introduction and distribution of plants in this region, the two most important are the mode of dispersal and the conditions for establishment. Hurricanes and violent winds, water, birds, and the activities of man, such as those utilizing airplanes, boats, bulldozers, and automobiles, are unquestionably primary sources of seeds, spores, and vegetative parts. But the establishment of a species depends primarily upon the availability of a suitable habitat. For instance, only those species that can grow at low elevations can become established in the Bahamas; the highest altitude is 208 feet on Cat Island. Many pteriodophytes need the protected, moist environment of solution pits or "banana holes" for their establishment, and these preferably should be in coppices.

Six species occur only in the Bahamian archipelago and in Florida. It is not possible to determine with absolute certainty the direction of their migration. But it is likely that they originated in the United States. These are *Pteris vittata* L., *Selaginella armata* Baker, *Tectaria lobata* (Poir.) Morton, *Thelypteris augescens*

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(Link) Munz & I. M. Johnst., and *T. ovata* R. St. John. *Osmunda regalis* var. *spectabilis* (Willd.) A. Gray, which also occurs rarely in Jamaica, should be placed in this category.

Only *Marsilea nashii* Underw. is strictly endemic in the region, from Great Inagua to Grand Turks.

Five other species are quite limited in their distribution and could be considered wide endemics. These include another sterile *Marsilea*, possible the Hispaniolan *M. berteroi* A. Br., from Acklin Island and South Caicos, *Anemia wrightii* Baker from Andros, also found in Cuba; *A. cicutaria* Kunze from Abaco, Andros and New Providence, also found in Cuba and Yucatán, *Selaginella bracei* Hieron. from Andros, also found in Cuba; and *Thelypteris cordata* (Fée) Proctor from Andros, also found in Jamaica. Apparently Cuba should be considered the point of origin for most of these species.

The remaining 30 species in the Bahamas also are found in Cuba, Hispaniola, and Puerto Rico. Many of these extend to islands in the Lesser Antilles, Jamaica, or even to Mexico, Central America, or South America. Most are found in southern Florida as well, with the exception of such species as *Polypodium squamatum* L. on Andros and *Schizaea poeppigiana* Sturm in dense coppices on Abaco. In my opinion, all of these have migrated northward into the Bahamian archipelago.

Those species that thrive best in association with the native pine *Pinus caribaea* Morelet (found on Abaco, Andros, Grand Bahama and New Providence, with a disjunct occurrence in the Caicos Islands) are *Anemia adiantifolia* (L.) Swartz, *Pteris longifolia* L., *Thelypteris normalis* (C. Chr.) Moxley, and *Pteridium aquilinum* var. *caudatum* (L.) Sadeb. The *Pteridium* frequently forms impenetrable masses in the "pineyards" on the northern islands. The northern *Osmunda regalis* var. *spectabilis* is found in fresh water marshes and ponds in the pinelands of Abaco. *Trismeria trifoliata* (L.) Diels is found in similar habitats on Grand Bahama and Abaco. *Blechnum serrulatum* L. C. Rich., *Acrostichum danaeifolium* Langsd. & Fisch., and *A. aureum* L. are found in less fresh water. All occasionally are found to some extent on islands devoid of pines, but they attain their optimum development when associated with pines.

Those islands or sections of islands devoid of pines, but which have an extensive coverage of broadleaf coppices, support various ferns in company with orchids and bromeliads. All occur on tree trunks, fallen logs, and on exposed rock ledges and walls. These are *Polypodium polypodioides* (L.) Watt, *P. heterophyllum* L., *P. phyllitidis* L. and its var. *latum* (Moore) Proctor, *P. plumula* Humb. & Bonpl. ex Willd., *Paltonium lanceolatum* (L.) Presl, and *Psilotum nudum* (L.) Pal. Beauv.

By far the greatest number of species occur in the solution pits, sink-holes, or "banana holes" that are formed in the limestone stratum common to all of the islands. The holes that support ferns usually occur in more shaded and more moist habitats than are found elsewhere on the islands. Although one or more species may often be found in these sinks, no single species can be said to occur in all fern-inhabited sinks. The four most frequently encountered are *Adiantum*

tenerum Swartz, *Tectaria lobata*, *Thelypteris normalis*, and *T. reptans* (J. F. Gmel.) Morton. In fact, some species are of singular occurrence and most are sporadic. These are *Pityrogramma calomelanos* (L.) Link on Andros, *Tectaria heracleifolia* (Willd.) Underw. on Grand Bahama and New Providence, and *Thelypteris dentata* (Forssk.) E. St. John on Great Exuma. Other such species with slightly more widespread distributions are *Adiantum melanoleucum* Willd., *Asplenium dentatum* L., *Psilotum nudum*, and *Sphenomeris clavata* (L.) Maxon.

The only genus of pteridophytes that might be considered a weed is *Nephrolepis*. The ruderal *N. exaltata* (L.) Schott is the most widespread, whereas *N. biserrata* (Swartz) Schott, *N. multiflora* (Roxb.) Jarrett ex Morton, and *N. rivularis* (Vahl) Mett. ex Krug are limited to only one or two localities.

A unique habitat, the leaf bases of old arborescent palmettos, is favored by two species: the rather widespread *Polypodium aureum* L. and the less common *Vittaria lineata* (L.) J. E. Smith, which is found only on Andros and New Providence. Although I have examined literally hundreds of palmettos hoping to find the Shoestring Fern, I have not been successful, mainly because most of the palms have been burned by malpais farming practices. My search for *Vittaria* recalls an interesting and most profitable trip that I made in company with Dr. E. T. Wherry and Mr. J. E. Benedict, Jr. in June, 1939, to central Georgia for the express purpose of seeing this species growing on clay cliffs. On our return northward into South Carolina, we visited the station for *Hymenophyllum tunbridgense* (L.) J. E. Smith in Oconee County, which I later reported (Amer. Fern J. **30:** 21-27, 1940). I have many fond memories of my various field trips and associations with Dr. Wherry.

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Spore Retention and Release from Overwintering Fern Fronds

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The need for ecological data on ferns is becoming increasingly apparent as more effort is directed toward an understanding of the significance of their morphological and physiological diversity (Wagner, 1973). If detailed ecological studies of fern sporophytes have to date been too few, such studies on the gametophyte generation are almost non-existent. The reproductive cycle of ferns has been known for over a century, and more than a thousand articles on fern gametophytes have been published, half of these in the last quarter century (Miller, 1968; Näf, 1975; Nayar & Kaur, 1971). However, nearly all data on gametophyte growth and sexual reproduction have been based on laboratory observations. Several factors have contributed to this paucity of information on gametophyte ecology, but perhaps the most important has been a widely held notion that gametophytes cannot be found in nature, or if found, cannot be identified. Several recent studies have indicated to the contrary, that *in situ* gametophyte studies not only are feasible, but that they are essential for the integration of existing laboratory data into studies on the natural history of ferns (Cousens, 1973; Holbrook-Walker & Lloyd, 1973; Lloyd, 1974; Farrar & Gooch, 1975).

To investigate further the feasibility of studying fern gametophytes in nature, we have begun a long-term observational study of fern reproduction in Woodman Hollow, a relatively isolated canyon in central Iowa, in which 13 species and 11 genera of ferns occur (see *Table 1*). This study is designed to answer the following questions. When are spores available for germination? When and where does reproduction occur and how is it influenced by micro- and macroclimates? When and by what breeding systems are sporophytes produced? Does sexual reproduction occur in nature on a regular basis for all species? Results of the first year of study (Farrar & Gooch, 1975) indicate that the data needed to answer these and other questions will be forthcoming. Here we report some unexpected data relevant to the question of when spores are available for germination.

Observations made on the time of spore maturation and first release during the growing season gave results which were similar to those of Hill and Wagner (1974) for pteridophytes in Michigan. Differences found in the two studies were no greater than might be expected due to differences in latitude, climate, habitat, and seasonal variation. Our observations also support their estimate that most spores of a given species are released during a period of about two weeks. However, a two week period of maximum release, if taken as a guide to the duration of spore release, may be very misleading. Our observations at Woodman Hollow indicate that for most species, significant quantities of spores are retained on the fronds after the initial release period and may be dispersed during a much longer period.

Only in *Botrychium virginianum* and *Osmunda claytoniana* were essentially all

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of the spores shed in a period as short as two weeks after spore maturation. These species have large, smooth-walled sporangia which mature simultaneously. Furthermore, these species have dimorphic pinnae, and the fertile pinnae wither and often disappear soon after maturation.

In the remainder of the species in our study, all sporangia in a sorus do not mature simultaneously. This differential maturation in itself lengthens the period of spore release, but an additional effect of this mixed sorus condition is that late-maturing sporangia are frequently covered by older, dehisced sporangia. As a result, they may be physically unable to dehisce and shed their spores normally, and often are prevented from opening at all. Thus, the sorus may remain indefinitely with a mixture of opened sporangia containing no spores (those which opened first), opened sporangia which still contain some or all of their spores, and unopened sporangia containing their full complement of spores.

Spore retention on the fern fronds varies among species and is dependent upon several factors. These include the number of sporangia per sorus, the presence of hairs or an indusium over the sorus, the type and degree of persistence of the indusium, and the time of maturation of the fertile frond. We observed a number of species which, after an initial flush of fertile fronds, continued to produce additional fertile fronds for the remainder of the growing season. Fronds maturing late in the season, especially of *Adiantum pedatum*, *Asplenium rhizophyllum*, and *Polypodium virginianum*, often had large numbers, occasionally approaching 100%, of unopened sporangia.

To quantify as much as possible this extended period of spore retention and release, fertile fronds of species in the study area were collected in December and again in March. The fronds were examined under a dissecting microscope and an estimate was made of the percent of unopened sporangia and the total number of spores remaining on the frond. Because of the generally deteriorated condition of the fronds, precise counts of sori, sporangia, and free spores could be made only with considerable difficulty. Thus, the spore estimates were limited to the orders of magnitude listed in *Table 1*. Ten or more sori were examined on each frond. The estimates of spores per frond were based on the number of unopened sporangia, the number of spores which could be removed from the dried frond, and the number of spores which could be seen remaining on the frond. Taking into account the inherent problems with the methodology of the spore assay and assuming that the estimates are not in error by more than an order of magnitude, it was obvious that for most species, large numbers of spores were retained on the fronds throughout the winter.

Spore viability was also tested for each collection by sowing the spores on mineral nutrient agar and measuring percent germination after three weeks. Germination in December ranged from 49% to 96%. Differences in germination percentages obtained in December and March probably represent variation between plants of the same species, since the overall range in March was similar (48–88%) to that in December and the number of species showing an increase was nearly as great as those showing a decrease in germination (*Table 1*). The change in *Cystopteris bulbifera* was most dramatic and may represent a real decrease in spore

viability for this species. To determine whether unopened sporangia of late-maturing fronds contained mature and viable spores, fronds of *Asplenium rhizophyllum* were divided into three lots on the basis of the number of unopened sporangia. These lots, when tested independently, showed similar germination percentages, indicating that indehiscence of sporangia, at least in this species, was not due to spore immaturity.

From December to March, a definite decrease in the number of unopened sporangia occurred only in late-maturing fronds of *Asplenium rhizophyllum*, which in December had greater than 90% unopened sporangia, and in *Matteuccia struthiopteris*, which was observed to be releasing spores both in December and in March. The total number of spores per frond appears generally to have remained relatively unchanged; however, our method of analysis may not have been sufficiently sensitive to detect the changes that did occur. That some spores were released from December to March is indicated by the decrease in unopened sporangia in *Asplenium rhizophyllum* and *Matteuccia struthiopteris* and by a measurable decrease in numbers of spores per frond in *Adiantum pedatum*, *Cystopteris bulbifera*, *Dryopteris goldiana*, and *Woodsia obtusa*.

TABLE 1. SPORE PRESENCE AND VIABILITY ON FERN FRONDS COLLECTED IN DECEMBER AND MARCH IN WOODMAN HOLLOW, IOWA

	No. fronds analyzed		*% sporangia unopened*		*No. spores/frond (× 1000)*		*% spore germination (number counted)*	
	Dec.	*Mar.*	*Dec.*	*Mar.*	*Dec.*	*Mar.*	*Dec.*	*Mar.*
Adiantum pedatum	6	3	1-10	same	10-100	1-10	77 (416)	67 (213)
Asplenium rhizophyllum	35	3	1-10	same	1-10	same	81 (237)	87 (378)
Asplenium rhizophyllum	6	—	10-20	—	10-100	—	84 (210)	—
Asplenium rhizophyllum	9	2	>90	>75	100-1,000	same	81 (308)	—
Athyrium filix-femina	3	4	1-10	same	10-100	same	49 (645)	73 (541)
Cryptogramma stelleri	0	2	—	>75	—	10-100	—	63 (183)
Cystopteris bulbifera	4	4	<1	same	1-10	0.1-1	62 (444)	6 (226)
Cystopteris fragilis	5	4	<1	same	1-10	same	68 (190)	58 (248)
Dryopteris goldiana	4	4	1-10	<1	10-100	1-10	50 (231)	48 (306)
Dryopteris spinulosa	4	4	<1	1-10	10-100	same	52 (307)	84 (703)
Matteuccia struthiopteris	3	1	>90	>80	100-1,000	same	96 (599)	95 (668)
Polypodium virginianum	3	5	10-50	same	100-1,000	same	70 (224)	88 (258)
Woodsia obtusa	6	4	1-10	same	10-100	1-10	82 (403)	59 (230)
Botrychium virginianum	no fertile fronds found							
Osmunda claytoniana	no fertile fronds found							

The data thus indicate that for most of the fern species in Woodman Hollow, sporophyte fronds of the previous year retain large numbers of spores throughout the winter and into the growing season of the following spring. Furthermore, it appears that some spores continue to be shed from these fronds as the winter progresses. The fate of the spores that are shed, or of those that remain on the fronds, has yet to be determined. The old, spore-bearing fronds are generally flattened against the substratum by early spring, and further release of their spores into air currents must be greatly reduced. Nevertheless, some spores could certainly germinate in the vicinity of the sporophyte fronds if a suitable habitat were available.

As yet, we have detected establishment of large numbers of gametophytes of only three species, *Adiantum pedatum, Cystopteris fragilis*, and *Woodsia obtusa*, and this has occurred in the fall. Our failure to observe gametophyte establishment of other species, or of these species at other times of the year, may be due to unfavorable weather conditions, or may reflect the inability of some species to reproduce regularly or extensively through the production of gametophytes. It most certainly reflects the rudimentary state of our knowledge of fern reproduction in nature. It may well be true that significant gametophyte establishment results only from spores released during the sporophyte growing season. However, until this is proven, workers studying gametophyte ecology in temperate areas must consider the possibility that significant reproduction may also result from spores shed from overwintering fronds.

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The Distribution and Abundance of Dryopteris in New Jersey

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The eastern American Wood Ferns are now reasonably well understood as to relationships. There is, however, little quantitative information concerning the local distribution, habitat preference, and abundance of *Dryopteris* hybrids, especially in the northeastern United States. The purpose of this investigation is to document the abundance, distribution, and habitat of the Wood Ferns found in New Jersey.

Although Wood Ferns are found throughout New Jersey, they are particularly common in the more rugged northwestern part of the state (Sussex, Passaic, Warren, and Morris Counties). Hybrids have been known since Dowell (1908) described *Dryopteris clintoniana* × *intermedia* and *D. goldiana* × *marginalis* from New Jersey. In "The Ferns of New Jersey" Chrysler and Edwards (1947) listed 14 hybrids and gave one record for each except *D.* × *boottii;* but no information was given about abundance, distribution, or habitat. Little specific information has been given by recent northeastern fern guides, although *Dryopteris* hybrids are listed and briefly discussed by Wherry (1961). Wagner (1963) discussed the relative abundance of species and hybrids of Wood Ferns in Virginia, and Britton (1965) tabulated their relative abundance in Ontario; no quantitative data were given.

Although hybrids are usually described as being rare, some fern hybrids are relatively common. Wagner (1969), in defense of the inclusion of hybrids in floras, pointed out that several Appalachian *Asplenium* hybrids are more common than the non-hybrid Hart's-tongue (*Phyllitis scolopendrium*), and that *Dryopteris* × *triploidea* and *D.* × *boottii* (both sterile hybrids) are commoner than either *D. celsa* or *D. clintoniana* (both fertile).

Herbarium records for *Dryopteris* hybrids are deceptive. Some of the hybrids are large and conspicuously different, and therefore frequently collected, whereas others are difficult to distinguish and less conspicuous, and so are less often taken. For this reason the abundance of hybrids was measured in two ways in this investigation: (1) the overall abundance, that is the number of stations at which each occurs in New Jersey as determined from herbarium records and field reconnaissance; and (2) the relative abundance as a proportion of the frequency with which a hybrid occurs when the parents are found growing together.

PROCEDURE

Populations of *Dryopteris* where hybrids might occur were located in three ways: (1) examining herbarium labels where reasonably exact data were given, (2) scanning topographic maps for likely habitat areas, and (3) extensive driving and hiking in the area where likely habitats might occur. Once a population had been

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located where two or more species of *Dryopteris* were growing intermixed, a careful search was made to locate all hybrids.

Identifying a plant of *Dryopteris* as a hybrid is usually not difficult; hybrids have abortive spores (Whittier & Wagner, 1971) and frequently sporangia as well, and are generally intermediate in morphology between their parents (see Wagner, 1971). Some hybrids are relatively easy to identify by morphology alone: those involving as parents *D. marginalis* (marginal sori and a dense tuft of tawny scales at the base of the stipes), *D. goldiana* (abrupt taper at the tips of the large blades and very dark, shiny basal scales), *D. intermedia* (glandular blades and indusia and twice pinnatifid pinnae), and *D. spinulosa* (eglandular blades and indusia and twice pinnatifid pinnae). The hybrid between *D. intermedia* and *D. spinulosa* can be distinguished from its similar parents by abortive spores (Tryon & Britton, 1966). Although spore abortion can often be determined with a 10× lens in the field, in this investigation spores were examined with a light microscope at 100×. The hybrids involving *D. celsa*, *D. clintoniana*, and *D. cristata* can be recognized as such, but determining parentage from morphology is often quite difficult. Chromosome counts and pairing behavior are very useful here. Slides were examined from both transplanted and wild plants, following methods given in Montgomery (1975). Voucher specimens for field and cytological studies were deposited in the Chrysler Herbarium of Rutgers University (CHRB), with duplicates in the herbarium of Upsala College (EONJ); duplicates are fronds from the same plant. For ranges and habitats, as well as abundance, material was examined from the following herbaria: AFS, CHRB, EONJ, MICH, NY, PENN, PH, US, and Staten Island Museum (SIM). Habitat information was tabulated from herbarium sheets where sufficient information was given.

RESULTS

Six species and 13 hybrids were found in field studies. The relative frequency of the hybrids was tabulated as a percentage of the number of populations where both parents were present (*Table 1*). The hybrid with the greatest frequency of occurrence when the parents were found together was *D. goldiana* × *marginalis* (100%), followed by *D. intermedia* × *spinulosa* (84%). It should be noted that the first combination of parents was found together only twice, whereas *D. intermedia* and *D. spinulosa* were found together 45 times.

The overall abundance of the species and hybrids, as determined from herbarium records (including the author's material) is given in *Table 2*. In this table a record refers to a distinct locality; duplicates from a locality at the same or different times are eliminated. *Dryopteris marginalis* was the most abundant species, from 176 localities. *D. intermedia* and *D. spinulosa* were nearly as abundant. The most abundant hybrids were *D. intermedia* × *spinulosa* and *D. cristata* × *intermedia*. Both of these, as well as *D. cristata* × *marginalis* were recorded from more stations than the least common species, *D. celsa*, *D. clintoniana*, and *D. goldiana*.

Chromosome counts made to verify taxa are given in *Table 3*. Additional counts from New Jersey were given by Montgomery (1975) and Wagner (1971).

TABLE 1. FREQUENCY OF *Dryopteris* PARENTS AND HYBRIDS IN NEW JERSEY FIELD POPULATIONS.

	× *cristata*		× *goldiana*		× *intermedia*		× *marginalis*		× *spinulosa*	
	n	*f*(%)	*n*	*f*(%)	*n*	*f* (%)	*n*	*f* (%)	*n*	*f* (%)
D. clintoniana	17	58.8	2	50.0	15	40.0	12	25.0	15	26.7
D. cristata			2	50.0	31	58.1	18	55.6	35	17.1
D. goldiana					1	0.0	2	100.0	1	0.0
D. intermedia							27	3.7	45	84.4
D. marginalis									20	5.0

n = number of populations with both parents present.
f = percent of populations (n) where the hybrid was found.

TABLE 2. NUMBER OF LOCALITIES OF *Dryopteris* HYBRIDS IN NEW JERSEY FROM HERBARIUM RECORDS.

	Number of localities for species	*Number of localities for hybrids* × *clintoniana*	× *cristata*	× *goldiana*	× *intermedia*	× *marginalis*	× *spinulosa*
D. celsa	2	0	4	3	2	3	1
D. clintoniana	24		13	6	10	4	5
D. cristata	108			2	45	29	11
D. goldiana	19				1	11	0
D. intermedia	138					2	46
D. marginalis	176						2
D. spinulosa	139						

TABLE 3. CHROMOSOME COUNTS IN NEW JERSEY *Dryopteris*.

I	II	*Source of Material*[1]
	D. cristata	
0	81±1	25466c, Macopin, Passaic Co.
0	82	25473y, Green Pond, Passaic Co.
0	81±1	8250p, Wawayanda, Sussex Co.
	D. goldiana	
0	41	8155b, Netcong, Morris Co.
	D. intermedia	
0	41	25466f, Macopin, Passaic Co.
0	41	11423d, Wallpack, Sussex Co.
	D. cristata × *intermedia* (*D.* × *boottii*)	
123	0	25466b, Macopin, Passaic Co.
122±2	0-1	25466d, Macopin, Passaic Co.
123	0	10528g, Macopin, Passaic Co.
	D. cristata × *marginalis* (*D.* × *slossonae*)	
121±3	0	8250j, Wawayanda, Sussex Co.
123±2	0	10528m, Macopin, Passaic Co.
	D. cristata × *spinulosa* (*D.* × *uliginosa*)	
76	43	7870e, Swartswood, Sussex Co.
	D. intermedia × *spinulosa* (*D.* × *triploidea*)	
40±1	40±2	66010c, Greendell, Sussex Co.

[1] Collected by the author; voucher at CHRB.

DISCUSSION

In general hybrids were found with both parents nearby, usually in sight. Occasionally, however, a hybrid plant was found with only one parent very close by. *Dryopteris* × *triploidea* was found six times with only *D. spinulosa* present; *D.* × *boottii* was found once with *D. cristata* about 0.25 mile away and no *D. intermedia* in the vicinity, and one other time with only *D. cristata* present. Wagner (1971) referred to this phenomenon as "hybridization by remote control," and it presumably happens when a spore from the missing parent is blown into the vicinity of the gametophyte of the other parent so that cross-fertilization can occur. Extinction of one species or the other, or both, at a locality after hybrid formation is another possible mechanism; the hybrid can persist and even spread slowly by rhizome growth. These conditions are unusual, however, and so parent species are usually found in the vicinity of the hybrids.

The abundance of the hybrids would be expected to be related to the abundance of the parental taxa. The quantitative information presented here indicates that this is true in some cases; thus, hybrids involving *D. goldiana* are rare in New Jersey. *Dryopteris intermedia* × *spinulosa* (*D.* × *triploidea*) and *D. cristata* × *intermedia* (*D.* × *boottii*) were common, and the parent species were very common. These were also the only taxa involved in "remote control" hybridization.

Hybrids were also more common if the parents had similar habitat preferences. *Dryopteris clintoniana* × *cristata* was found relatively frequently, both in herbarium records (*Table 2*), although often identified as one or the other parent, and in relative abundance in field studies (*Table 1*). Both parents occupied similar swampy habitats. On the other hand, *D. clintoniana* × *marginalis* was relatively uncommon, and these parents occupied rather different habitats. The most spectacular hybrid populations occurred where a wooded ridge occupied by *D. intermedia* and *D. marginalis* sloped into a wooded swamp occupied by *D. clintoniana*, *D. cristata*, and *D. spinulosa*. In such locations the edge of the swamp may be virtually lined with hybrids! At Big Spring, where *D. goldiana* also occurred, six of 15 possible hybrids were found and the number of hybrid plants was unusually great. In two other areas, Wawayanda and Macopin, five species were present and six of ten possible hybrids were found.

Certain hybrids were inexplicably rare. The most notable case was *D. intermedia* × *marginalis*. The parental species were abundant and occupied similar habitats, and so large intermixed populations were encountered frequently. This hybrid is also relatively easily seen if the population is searched carefully. The same general situation applies to *D. cristata* × *spinulosa* in New Jersey. No explanation is known for the lack of hybridization between these species. Experimental studies with the gametophytes may be helpful.

The relative abundance of hybrids found in New Jersey agrees in general with that found in Virginia by Wagner (1963) and in Ontario by Britton (1965). Both reported *D. intermedia* × *spinulosa* as the commonest hybrid combination, as in the present study. Both stated that *D. intermedia* × *marginalis* and *D. marginalis* × *spinulosa* were rare, as documented here. Britton listed *D. cristata* × *mar-*

ginalis as "rare to very rare" in Ontario; in New Jersey it was recorded from 29 stations (third highest) and found 55.6% of the time when the parents were found growing together. *Dryopteris clintoniana* × *intermedia* was also more frequent in New Jersey than in Ontario.

The distribution, habitat preference, and abundance of each *Dryopteris* species and hybrid in New Jersey are summarized below.

Dryopteris celsa (W. Palmer) Small. Very rare, perhaps extinct. Known from four localities in Bergen County (two by hybrids only); all from swamps that have been destroyed by urbanization.

Dryopteris clintoniana (D. C. Eaton) Dowell. Uncommon. In low woods or wooded swamps; several locations in Sussex County, and a few each in Passaic, Warren, Morris, and Essex Counties.

Dryopteris cristata (L.) Gray. Common. Usually in wooded swamps, growing on old stumps, logs, and hummocks; occasionally in wet meadows or damp woods; recorded from all counties except Hudson and Cumberland, but more common in the northern part of the state.

Dryopteris goldiana (Hook.) Gray. Uncommon. In rich woods or ravines, especially on limestone in New Jersey; several records (mostly old) for Sussex and Warren Counties, and one or two each in Bergen, Morris, Essex, and Hunterdon.

Dryopteris intermedia (Muhl.) Gray. Abundant. Rocky, wooded slopes, especially north- or east-facing, sometimes in wet woods or swamps especially in the southern half of the state; known from all 21 counties.

Dryopteris marginalis (L.) Gray. Abundant. Rocky woods, often drier than *D. intermedia*, and only rarely in swamps; recorded from all counties except Cape May.

Dryopteris spinulosa (O. F. Muell.) Watt. Abundant. In woods, nearly always in moist areas (springs, etc.), or in wooded swamps as *D. cristata*. Recorded from all counties except Union.

Dryopteris celsa hybrids. Five hybrids involving *D. celsa* are recorded from New Jersey: *D. celsa* × *cristata*, *D. celsa* × *goldiana*, *D. celsa* × *intermedia* (*D.* × *separabilis* (Palmer) Small), *D. celsa* × *marginalis* (*D.* × *leedsii* Wherry), *D. celsa* × *spinulosa*; all from Bergen County (Montgomery, 1975).

Dryopteris clintoniana × *cristata*. Uncommon. In swamps, as the parents, but only a few plants; recorded from Sussex, Passaic, Warren, and Morris Counties.

Dryopteris clintoniana × *goldiana*. Uncommon. Edges of swamps with *D. goldiana* above and *D. clintoniana* below; recorded from Sussex, Passaic, Warren, and Essex Counties.

Dryopteris clintoniana × *intermedia* (*D.* × *dowellii* (Farw.) Wherry). Uncommon; edges of swamps or wet woods; type from Macopin, Passaic County, plus several other records in Sussex and Morris Counties.

Dryopteris clintoniana × *marginalis*. Rare. In swamps; three localities in Sussex County, one in Warren County.

Dryopteris clintoniana × *spinulosa* (*D.* × *benedictii* Wherry). Rare. In swamps; five records in Sussex, Passaic, and Morris Counties.

Dryopteris cristata × *goldiana*. Doubtfully present. One sterile collection from Lodi, Bergen County, which could be a *D. celsa* hybrid, and a possible plant from Morris County.

Dryopteris cristata × *intermedia* (*D.* × *boottii* (Tuckerm.) Underw.). Common. Most commonly in swamps or wet woods, but also on wooded slopes, or even on rock walls; occasionally several plants, but more commonly only a few; most of the northern counties, plus Gloucester and Cape May.

Dryopteris cristata × *marginalis* (*D.* × *slossonae* Wherry). Common. Edges of swamps, nearly always on hummocks or stumps; recorded from all northern counties, plus Mercer, Middlesex, and Monmouth in central New Jersey.

Dryopteris cristata × *spinulosa* (*D.* × *uliginosa* Druce). Uncommon. In swamps, rarely more than one or two plants; four localities in Sussex, and one or two each in Passaic, Bergen, Morris, Middlesex, Monmouth, and Burlington Counties.

Dryopteris goldiana × *intermedia*. Rare. One record in Bergen County from an area now destroyed.

Dryopteris goldiana × *marginalis* (*D.* × *neowherryi* Wagner). Uncommon. At borders of swamps or in damp rich woods; several records in Sussex County, plus two each in Bergen and Morris Counties, and one in Hunterdon County.

Dryopteris goldiana × *spinulosa*. Unknown in the state.

Dryopteris intermedia × *marginalis*. Rare. Only two records: in 1914 from Sussex County, and by the author in 1973 in Union County; the latter with the parents on a steep, northwest-facing slope in hemlock woods.

Dryopteris intermedia × *spinulosa* (*D.* × *triploidea* Wherry). Common. In woods, especially open areas such as pine plantations, or edges of swamps, banks of streams, etc.; the commonest hybrid, frequent with the parents and sometimes outnumbering either or both; recorded from nine counties, mostly in the northern part of the state.

D. marginalis × *spinulosa* (*D.* × *pittsfordensis* Slosson). Rare. Only two records, one from a swamp in Middlesex County, the other, possibly from cultivated plants, in Monmouth County.

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Cystopteris bulbifera in the Southwestern United States

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The Bulblet Fern occurs primarily in eastern North America and reaches its southwestern distributional limit in Arizona (*Fig. 1*). The eastern distribution is fairly continuous as far west as the eastern edge of the Great Plains, where populations become sporadic. A gap of about 1000 km separates known localities in eastern Nebraska and Oklahoma from sites in New Mexico and Texas (Wagner, 1972). Anderson (1974) discussed the distribution of this species in the Great Plains but not in the Southwest. *Cystopteris bulbifera* (L.) Bernh. is known in Texas only in the Guadalupe Mountains, Culberson Co. (Correll & Johnston, 1970). New Mexican collections have been made in these same Guadalupe Mountains, Otero or Eddy Co. (Blasdell, 1963, p. 67); in the White Mountain wilderness, northern Otero Co. (C. R. Hutchins, pers. comm.); and north of Taos, Taos Co. (Dittmer, et al., 1954, p. 28). In Utah, Flowers (1944) reported the species from Zion National Park, Washington Co.; Elk Mountain, San Juan Co.; and Brighton and Little Cottonwood Canyon, Salt Lake Co. There are no reports of this species from Colorado, Nevada, or farther north. In Arizona, *C. bulbifera* has previously been known only from the West Fork of Oak Creek Canyon, Coconino Co. (Kearney, et al., 1960, p. 44). I have recently collected specimens of it in Walnut Canyon, Coconino Co., at a site about 40 km northeast of the Oak Creek locality. A recent floristic study of Walnut Canyon by Joyce (1974) does not mention the occurrence of *C. bulbifera*, but my examination of his collections has revealed one specimen of this species (*Joyce WC634*, ASC) misidentified as *C. fragilis* (L.) Bernh.

Blasdell (1963, p. 28) stated that *C. bulbifera* usually grows on neutral soils associated with limestone, whereas Anderson (1974) indicated that in Nebraska it occurs on sandstone. In Arizona, I have collected this species on both substrates. *Cystopteris bulbifera* is abundant in the lower portion of the West Fork of Oak Creek Canyon (1550 m), occurring in large colonies on the red sandstone talus and cliffs capped by Kaibab limestone. Associated fern species are *Adiantum capillus-veneris*, *A. pedatum*, and *Polypodium hesperium*. At higher elevations in the canyon (2000 m), where *Cystopteris fragilis*, *Dryopteris filix-mas*, and *Polystichum lonchitis* are found, the Bulblet Fern occurs on limestone outcrops and boulders. At Walnut Canyon, *C. bulbifera* occurs in a few small colonies at 1800 m in the narrow gorge to the southwest of the Walnut Canyon National Monument Headquarters. Here, the plants grow in shaded seepage sites on vertical cliffs of Kaibab limestone. Associated species are *Cheilanthes feei*, *Cystopteris fragilis*, and *Selaginella underwoodii*. Putative hybrids between *C. bulbifera* and *C. fragilis* from Walnut Canyon are currently under investigation.

Since the only previously reported chromosome counts for *C. bulbifera* were based on specimens from eastern North America, an attempt was made to obtain

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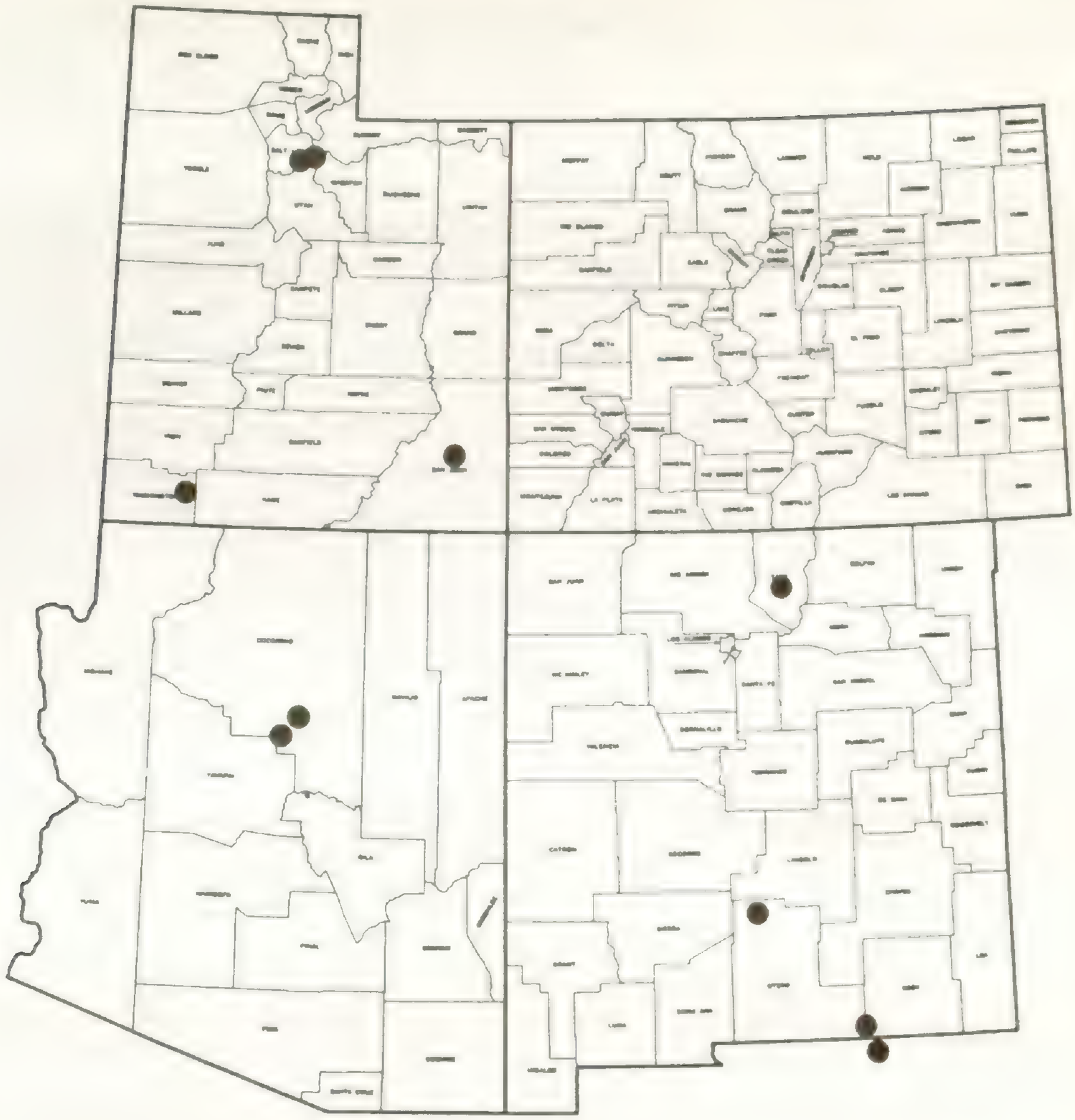

FIG. 1. Known distribution of *Cystopteris bulbifera* in the southwestern United States.

FIG. 2. Camera lucida drawing of meiotic chromosomes of *Cystopteris bulbifera* at metaphase I showing 42 pairs of chromosomes (Walnut Canyon, Coconino County, Arizona, *Reeves 3030A*, ASU).

counts on Arizona material. Specimens of this species were collected in both Oak Creek and Walnut Canyons on 17 June 1975. Pinnae were fixed in modified Carnoy's fixative (6 chloroform: 4 ethanol: 1 glacial acetic acid). After 24 hours the material was transferred to 70% ethanol and refrigerated until studied. Developing sporangia were stained in iron aceto-carmine and squashed in Hoyer's medium. All cells studied had normal chromosome pairing with $2n = 42$ pairs (*Fig. 2*). This agrees with all previously reported counts for the species (*Table 1*). The counts reported here are the first reports for *C. bulbifera* in the western United States, indicating that this species apparently occurs as a diploid throughout its range.

TABLE 1. CHROMOSOME NUMBERS IN *Cystopteris bulbifera*.

Number	*Voucher or reference*	*Locality*
$n = 42$	Britton (1953)	Canada: Ontario
42	Wagner (1955)	Ohio: Ross Co.
42	Wagner (1955)	Michigan: Oakland Co.
42	Wagner & Hagenah (1956)	Michigan: Ionia Co.
42	Wagner & Hagenah (1956)	Michigan: Eaton Co.
42	Reeves *3026A* (ASU)	Arizona: Walnut Canyon, Coconino Co.
42	Reeves *3030A* (ASU)	Arizona: Walnut Canyon, Coconino Co.
42	Reeves *3046D* (ASU)	Arizona: Oak Creek Canyon, Coconino Co.

I am grateful to Dr. W. H. Wagner, Jr. for his suggestion that the genus *Cystopteris* be studied carefully in Arizona. I wish to thank the Superintendent of Walnut Canyon National Monument for granting permission to collect plants. I express my gratitude to the curators of Arizona herbaria (ARIZ, ASC, ASU, and MNA) for use of their facilities and the loan of specimens. Doctors D. J. Keil, D. J. Pinkava and W. H. Wagner, Jr. have reviewed this manuscript and their assistance is gratefully acknowledged.

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Variation in North American Asplenium platyneuron

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One of the most common and widespread of the eastern North American spleenworts is the Ebony Spleenwort, *Asplenium platyneuron* (L.) Oakes ex D. C. Eaton, which ranges from Quebec to Ontario, south to Colorado, Texas, Florida, and the West Indies. It is also known from South America and South Africa (Mohlenbrock, 1967, p. 157). Because it is a common, attractive, and variable species, a number of varieties and forms have been recognized by both professional pteridologists and amateur fern enthusiasts. We have found the literature to contain nine infraspecific names accounting for variations in frond and pinna form or in stipe and rachis branching or proliferations. The purpose of this paper is to account historically for these taxa, to review their taxonomy and nomenclature, and to provide a key for their identification. The stimulus for this report comes from the discovery of the striking cut-leaf variant *A. platyneuron* f. *hortonae*, which is reported here for the first time from Illinois. Our studies have revealed that much herbarium material of *A. platyneuron* is incompletely or incorrectly determined below the species level.

KEY TO INFRASPECIFIC TAXA OF NORTH AMERICAN ASPLENIUM PLATYNEURON

1. Stipe and rachis unbranched and not proliferous.
   2. Longest pinnae less than 3.5(4) cm long; pinnae subentire to nearly pinnatisect; erect fronds with or without sori.
      3. Pinnae subentire to crenulate or serrulate ..... 1a. var. *platyneuron*
      3. Pinnae doubly serrate to deeply incised or pinnatifid to pinnatisect.
         4. Pinnae doubly serrate to deeply incised; all or nearly all of the pinnae cut less than 4/5 of the way to the midvein; erect fronds normally soriferous ..... 1b. var. *incisum*
         4. Pinnae pinnatifid to pinnatisect; all or nearly all of the pinnae cleft more than 4/5 of the way to the midvein; fronds without sori ..... 1c. f. *hortonae*
   2. Longest pinnae more than 3.5 cm long; pinnae often coarsely serrate-incised; erect fronds normally soriferous ..... 1d. var. *bacculum-rubrum*
1. Stipe and/or rachis branched or proliferous.
   5. Stipe and/or rachis branched ..... 1e. f. *furcatum*
   5. Stipe and/or rachis proliferous ..... 1f. f. *proliferum*

1a. Asplenium platyneuron (L.) Oakes ex D. C. Eaton var. platyneuron, Ferns No. Amer. 1: 24. 1878.

Acrostichum platyneuros L. Sp. Pl. **2:** 1069. 1753.
Asplenium ebeneum Ait. Hort. Kew. **3:** 462. 1789.
Chamaefilix platyneuros (L.) Farw. Amer. Midl. Nat. **12:** 269. 1931.

Most American botanists in the nineteenth century chose to use Aiton's name *A. ebeneum* for this species. Fernald (1935, pp. 382–384) discusses the difficulties in typifying *Acrostichum platyneuros*.

Typical *A. platyneuron* has erect fertile fronds up to 40 cm long with as many as 50 pairs of pinnae (Fernald, 1950) and a lustrous, dark brown, unbranched stipe

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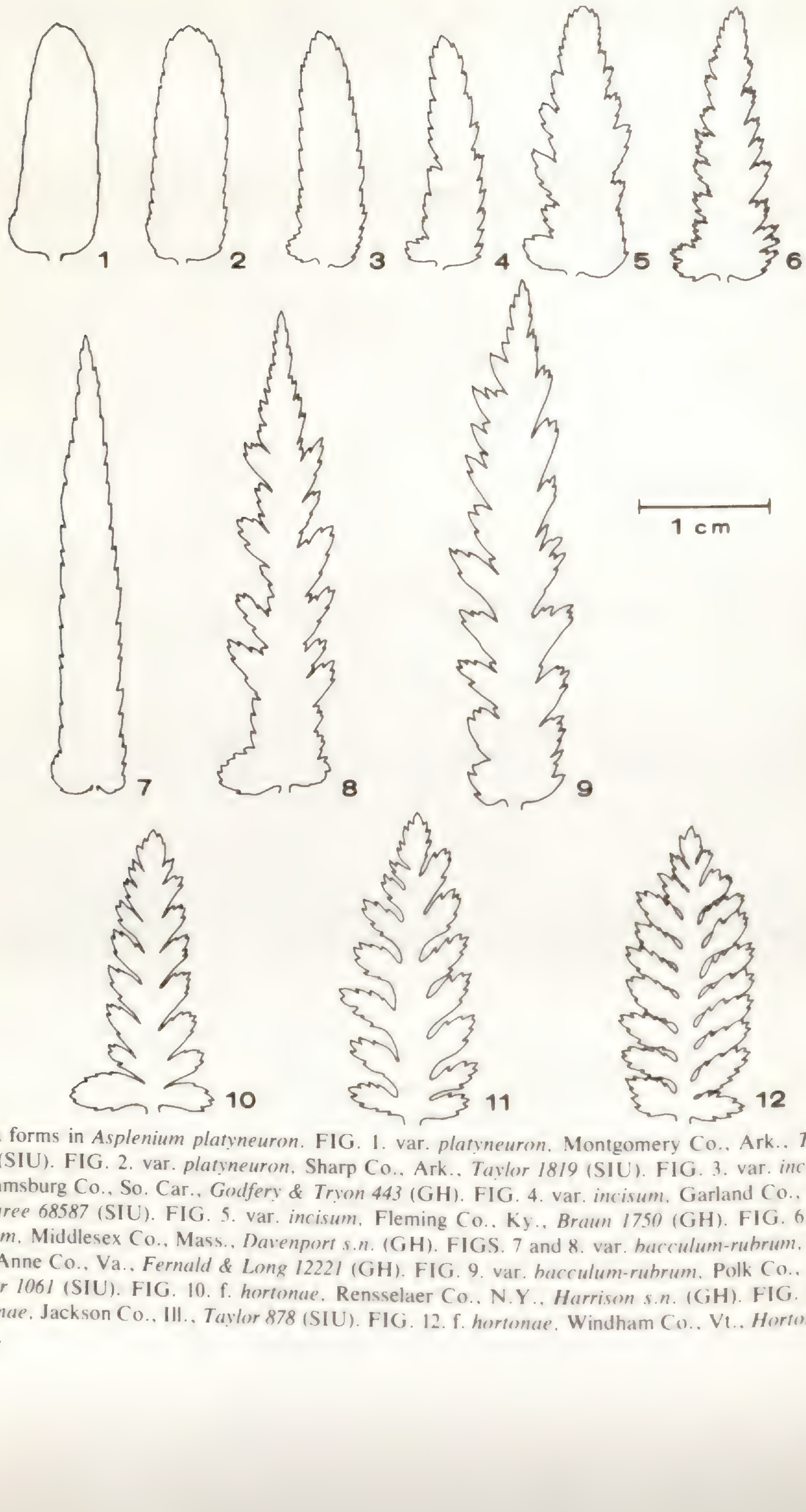

Pinna forms in *Asplenium platyneuron*. FIG. 1. var. *platyneuron*, Montgomery Co., Ark., *Taylor 1073* (SIU). FIG. 2. var. *platyneuron*, Sharp Co., Ark., *Taylor 1819* (SIU). FIG. 3. var. *incisum*, Williamsburg Co., So. Car., *Godfery & Tryon 443* (GH). FIG. 4. var. *incisum*, Garland Co., Ark., *Demaree 68587* (SIU). FIG. 5. var. *incisum*, Fleming Co., Ky., *Braun 1750* (GH). FIG. 6. var. *incisum*, Middlesex Co., Mass., *Davenport s.n.* (GH). FIGS. 7 and 8. var. *bacculum-rubrum*, Princess Anne Co., Va., *Fernald & Long 12221* (GH). FIG. 9. var. *bacculum-rubrum*, Polk Co., Ark., *Taylor 1061* (SIU). FIG. 10. f. *hortonae*, Rensselaer Co., N.Y., *Harrison s.n.* (GH). FIG. 11. f. *hortonae*, Jackson Co., Ill., *Taylor 878* (SIU). FIG. 12. f. *hortonae*, Windham Co., Vt., *Horton s.n.* (GH).

and rachis *(Fig. 13)*. The blade is linear-oblong or linear-oblanceolate. Medial pinnae are oblong to oblong-lanceolate and auriculate at the base on their upper and also often on their lower margins. In addition, the pinnae are serrulate and rarely over 2 cm long (*Figs. 1-3*). Fernald (1950) described typical *A. platyneuron* as having "pinnae minutely crenulate, dentate or fine serrulate"; Morton (1952) referred to the pinnae of sterile fronds as "remotely serrulate" and those of the fertile fronds as "serrate."

1b. Asplenium platyneuron var. incisum (Howe ex Peck) B. L. Robins. Rhodora 10: 29. 1908.

Asplenium ebeneum var. *incisum* Howe ex Peck, Ann. Rep. Regents Univ. N.Y. **22:** 104. 1869. TYPE: Poestenkill, Rennselaer County, New York, *E. C. Howe* (NYS, photos GH!).

Asplenium ebeneum var. *serratum* E. S. Miller, Bull. Torrey Bot. Club **4:** 41. 1873. TYPE: Wading River, Suffolk Co., New York, *E. S. Miller* (not located).

Asplenium platyneuron var. *serratum* (E. S. Miller) B. S. P. Prelim. Cat. Pl. New York 73. 1888.

Asplenium ebeneum f. *serratum* (E. S. Miller) Clute, Our Ferns 314. 1901.

Asplenium platyneuron f. *serratum* (E. S. Miller) R. Hoffm. Boston Soc. Nat. Hist. **36:** 193. 1922.

Chamaefilix platyneuros var. *serrata* (E. S. Miller) Farw. Amer. Midl. Nat. **12:** 270. 1931.

The first variation based on pinna characters was described in 1869 by Peck as var. *incisum:* "In this form the pinnae are about one inch long, and all except the extreme upper and lower ones are deeply incised-pinnatifid; the pinnules are rather strongly 3-5 crenate toothed. I have thought best to give it the name suggested by its discoverer [Howe]." Howe's type material does posses several nearly pinnatifid pinnae; however, most of the pinnae are doubly serrate or serrate-incised. It appears that the doubly serrate or serrate-incised to nearly pinnatifid pinnae separate var. *incisum (Figs. 4-6)* from var. *platyneuron*, although numerous intermediates are readily found.

Essentially the same taxon was described by Miller ". . . with the fronds wider than usual and the segments very sharply serrate, which he [Miller] proposes to ticket at Dr. Gray's suggestion as var. *serratum*." Although we have been unable to locate Miller's specimens, an examination of authentic material, as determined by Asa Gray, indicates that both var. *serratum* and var. *incisum* are referable to the same variety.

1c. Asplenium platyneuron f. hortonae (Davenp.) L. B. Smith, Rhodora 30: 14. 1928.

Asplenium ebeneum var. *hortonae* Davenp. Rhodora **3:** 1. 1901. TYPE: Brattleboro, Windham County, Vermont, Sept. 1900, *F. B. Horton s.n.* (isotypes GH!, US).

Asplenium ebeneum f. *hortonae* (Davenp.) Clute, Fern Bull. **14:** 86. 1906.

Asplenium platyneuron var. *hortonae* (Davenp.) Clute, Fern Bull. **17:** 21. 1909.

Asplenium platyneuron f. *dissectum* Bened. Amer. Fern J. **37:** 11. 1947. TYPE: Lanedon, St. Mary's County, Maryland, 21 Oct 1945, *J. E. Benedict 5230* (US!).

Mrs. Francis B. Horton first found the feathery-fronded form of *A. platyneuron* in September, 1900, in Brattleboro, Vermont. She sent material to Davenport, who described it as *A. ebeneum* var. *hortonae*. Davenport commented that the plant was so different in appearance that he first thought it to be a new species.

Asplenium platyneuron f. *hortonae* has been found only sterile. Its pinnae are deeply pinnatifid to pinnatisect, with the ultimate segments ovate to oblong or

Frond forms in *Asplenium platyneuron*. FIG. 13. var. *platyneuron*, Montgomery Co., Ark., *Taylor 1073* (SIU). FIG. 14. f. *furcatum*, after Clute (1909). FIG. 15. f. "*multifidum*," Upshur Co., W. Va., *Tetrick s.n.* (WVA). FIG. 16. f. *proliferum*, after Marshall (1923).

obovate to spatulate and crenulate to serrulate-incised (*Figs. 10-12*). Due to its sporadic occurrence and distinctive appearance, Clute's treatment of this taxon as a form is quite logical, although some specimens approach var. *incisum* or var. *bacculum-rubrum*.

Asplenium platyneuron f. *hortonae* was found in Jackson County, Illinois, approximately 4 miles SW of Ava, SW ¼ of sect. 10, T8S, R4W, in July, 1971 (*Taylor 878*, SIU). A single plant occurs with several of var. *platyneuron* on a west-facing hillside woods dominated by *Quercus stellata*, *Q. velutina*, *Q. alba*, *Ulmus alata*, and *Carya ovalis*. Other species in the immediate vicinity of the plant include *Fraxinus americana*, *Ostrya virginiana*, *Eupatorium rugosum*, *Sanicula canadensis*, *Acalypha rhomboidea*, *Woodsia obtusa*, and *Botrychium dissectum* var. *obliquum*. The Illinois material of f. *hortonae* is sterile, with 22-28 pairs of deeply pinnatifid pinnae on fronds up to 35 cm long. The pinnae are up to 3.2 cm long, with the basal pair of lobes usually larger and often at right angles to the pinna midvein.

Benedict's f. *dissectum* is based on a large and much-divided specimen of *A. platyneuron*. Although three fronds of the Benedict specimen bear pinnae that are more divided than those of type material of f. *hortonae*, the other fronds are typical for f. *hortonae*. In addition, the Benedict specimen is sterile like those of all collections of f. *hortonae*. On the basis of pinna length alone, Benedict's collection, with pinnae up to 4 cm long, would fit the dimensions of var. *bacculum-rubrum*. However, its sterility and pinna dissection place it clearly with f. *hortonae*.

1d. Asplenium platyneuron var. bacculum-rubrum (Featherm.) Fern. Rhodora 38: 304. 1936.

Asplenium ebeneum var. *bacculum-rubrum* Featherm. Rep. Bot. Surv. So. Centr. Louisiana **1870**: 75. 1871. TYPE: Near Baton Rouge, Louisiana, *Featherman* (not located).

Asplenium platyneuron var. *euroaustrinum* Fern. Rhodora **37**: 382. 1935. TYPE: Munden, Princess Anne County, Virginia, 1 Aug 1934, *Fernald & Long 3603* (GH; isotype US).

Featherman described *A. ebeneum* var. *bacculum-rubum* from plants found near Baton Rouge, Louisiana as follows: "Stipe and rachis purplish brown, glossy, tall, one to two feet high. Fronds linear, lanceolate, accuminate, pinnate. Pinnae numerous, sessile, auricled on both sides of the base, coarsely serrate, the pinnae below the middle gradually decreasing in length. Fruit-dots elongated, from twenty to thirty on each pinna. Pinnae distinct."

A year after Fernald described var. *euroaustrinum*, Fernald corrected his error when he made the combination *A. platyneuron* var. *bacculum-rubrum* (Featherm.) Fern. This mainly southern variety has fertile fronds which are up to 70 cm long, with each frond bearing up to 70 pairs of pinnae. The pinnae are frequently coarsely serrate-incised and are typically longer than 3.5 cm (*Figs. 7-9*). The entire aspect of this variety is coarser than that of var. *platyneuron* and, at its extremes, is found to intergrade with var. *incisum*.

1e. Asplenium platyneuron f. furcatum Clute, Fern Bull. 17: 89. 1909.

Asplenium platyneuron f. *multifidum* Tetrick, Amer. Fern J. **39**: 92. 1949. TYPE: Upshur County, West Virginia, 21 June 1946, *R. M. Tetrick II* (WVA!).

TYPE: Asheville, Buncombe County, North Carolina, *Wright* (not located).

Clute's f. *furcatum* is based on a collection sent to him from Asheville, North Carolina by Miss Frances M. Wright and about which he states, "The plant was normal in all respects with the exception of the fronds . . . which were much branched at the apex." An illustration accompanies Clute's description (*Fig. 14*).

Apparently unaware of Clute's description, Tetrick described f. *multifidum* stating, "fronds much branched, the ultimate divisions crested." Comparing the holotype of f. *multifidum* with Clute's illustration of f. *furcatum* (*Figs. 14* and *15*), it appears that these two forms are essentially the same.

1f. Asplenium platyneuron f. proliferum (D. C. Eaton) Tanger, Amer. Fern J. 23: 16. 1933.

Asplenium ebeneum var. *proliferum* D. C. Eaton, Bull. Torrey Bot. Club **6:** 307. 1879. TYPE: Near Ocala, Marion County, Florida, Mar–Apr 1879, *Capt. J. D. Smith.* (isotype US).

Asplenium ebeneum f. *proliferum* (D. C. Eaton) Clute, Fern Bull. **14:** 86. 1906.

D. C. Eaton described var. *proliferum* from specimens collected by Captain J. D. Smith near Ocala, Florida. Proliferous plantlets are normally quite small, inconspicuous, and located near the base of the frond (*Fig. 16*). They have been noted on taxa otherwise referable to var. *platyneuron*, var. *incisum*, or var. *bacculum-rubrum*.

The authors are grateful to Dr. Delzie Demaree, Dr. Karl Schwaab, and Mr. John White for their aid in this study.

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The Distribution of Dryopteris spinulosa and its Relatives in Eastern Canada

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There are some excellent distribution maps of vascular plants from Quebec and Labrador in Rousseau (1974). However, his map for *Dryopteris spinulosa* (O. F. Muell.) Watt actually groups data for all the species of *Dryopteris* which have been referred to as the *D. spinulosa* complex, much as Boivin (1966) did when considering *D. austriaca* (Jacq.) Woynar. This conceals the interesting geographic patterns found in eastern North America, where there are three northern limits in Quebec and Labrador and one southern limit. Biosystematists (Wagner, 1971; Wherry, 1961) recognize two diploid species and two tetraploid species in this complex. The diploids are *D. intermedia* (Muhl.) A. Gray and *D. assimilis* S. Walker (which also has been called diploid *D. dilatata* or diploid *D. spinulosa* var. *americana)*. The tetraploids are *D. spinulosa* (O. F. Muell.) Watt (sometimes called *D. carthusiana* (Villar) H. P. Fuchs) and *D. campyloptera* Clarkson.

After determining that the northern Clay Belt plants near Amos were in fact diploid and not tetraploid *D. campyloptera* as expected (Britton, 1967), I decided in the tradition of Wherry to attempt to delineate the ranges of the *D. spinulosa* complex species in Quebec, and more specifically to see if the ranges of the diploid *D. assimilis* and the tetraploid *D. campyloptera* overlapped. For studies of genomic analysis and chromatography, a concerted effort was made to find hybrids between these four species of the complex, which were found growing together at Métis and Mt. Albert in 1968. *Dryopteris assimilis* was looked for unsuccessfully in Prince Edward Island, Nova Scotia, and New Brunswick in 1970. In 1971 *D. campyloptera* was studied in Vermont and north in the Laurentians to St. Donat de Montcalm and Mt. Tremblant. In 1972 I collected material north of Quebec City and along the north shore of the St. Lawrence River to Sept Iles and from there to Labrador City. The cytological vouchers, which represent over 200 different plants, have supplied material for chemotaxonomic studies (Widén & Britton, 1971; Britton & Widén, 1974; Widén et al., 1975), and are a sample from which extrapolations can be made to similar phenotypes for the purpose of mapping. The maps in this paper have been prepared from selected specimens seen in the following herbaria: GH, MTMG, MT, MTJB, QFA, QUE, QMP, SFS, ULF.

Dryopteris intermedia.—There are scattered collections of this species (*Fig. 1*) from the boreal forest, but it is much more abundant in the mixed forests (maple-beech) in southwestern Quebec. One station with cytological specimens is near Amos (ca. 48° 30′ N), which is near the northern limit of its range (ca. 50° N). Only four stations are plotted north of this latitutde. Ferns with a similar distribution mapped by Rousseau (1974) with their respective map numbers are: *Osmunda cinnamomea* 28, *Osmunda regalis* 30, *Dryopteris cristata* 46, and *Pteridium aquilinum* 67.

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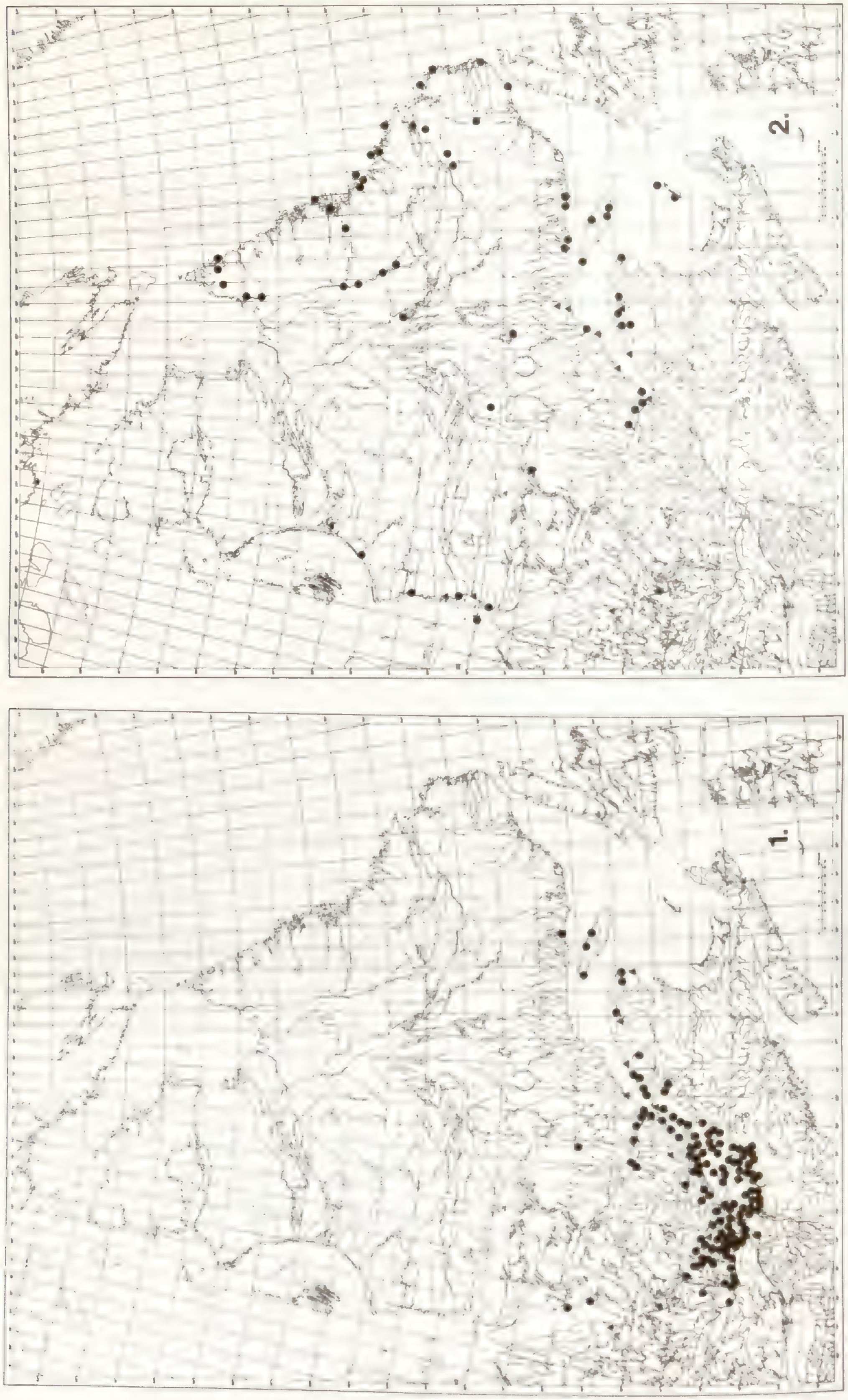
[1]The author thanks the National Research Council of Canada for financial support for this research.



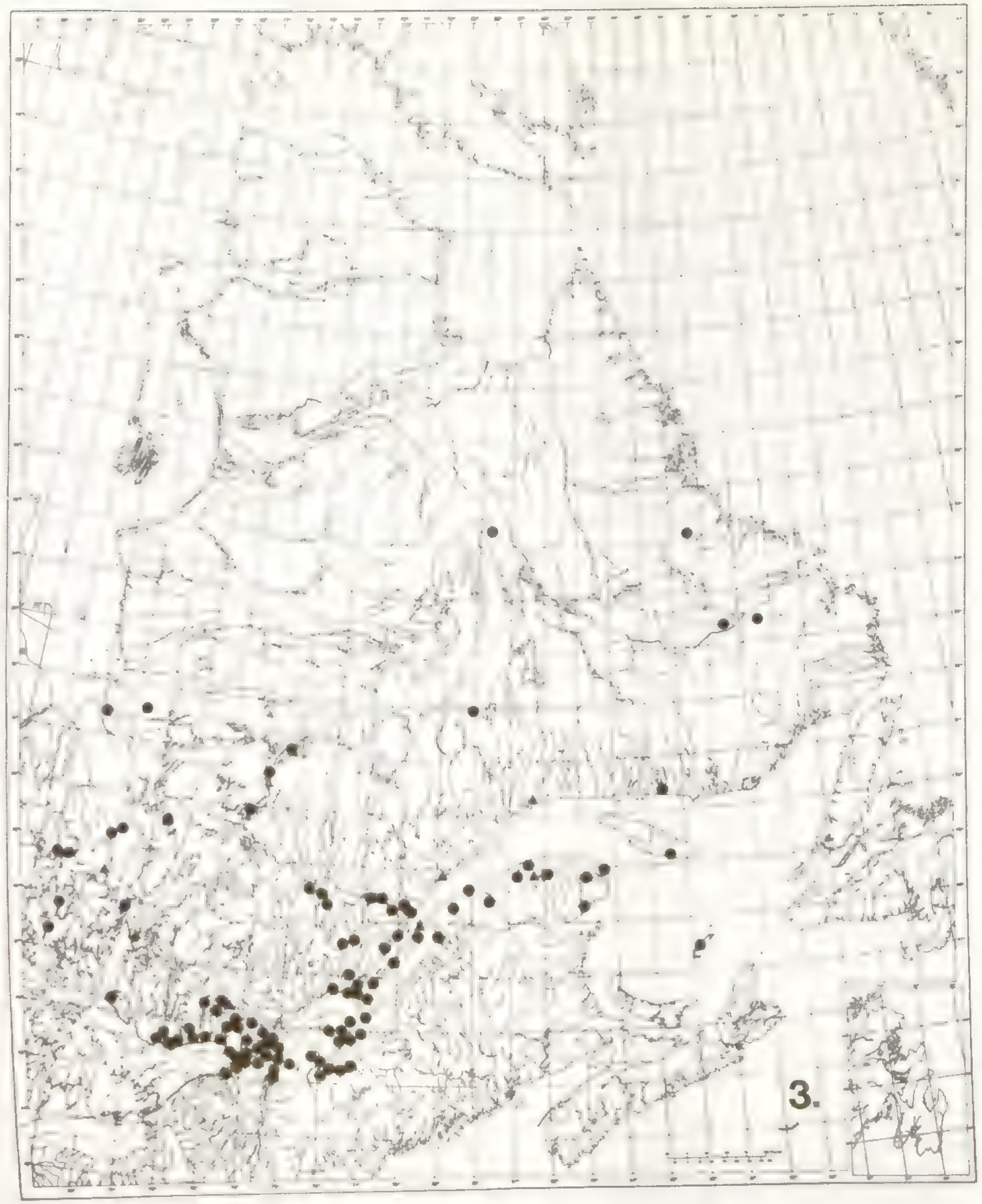
Distribution of *Dryopteris* in Quebec and Labrador. FIG. 1. *D. intermedia*. FIG. 2. *D. assimilis*. ▲ = collections cytologically determined.

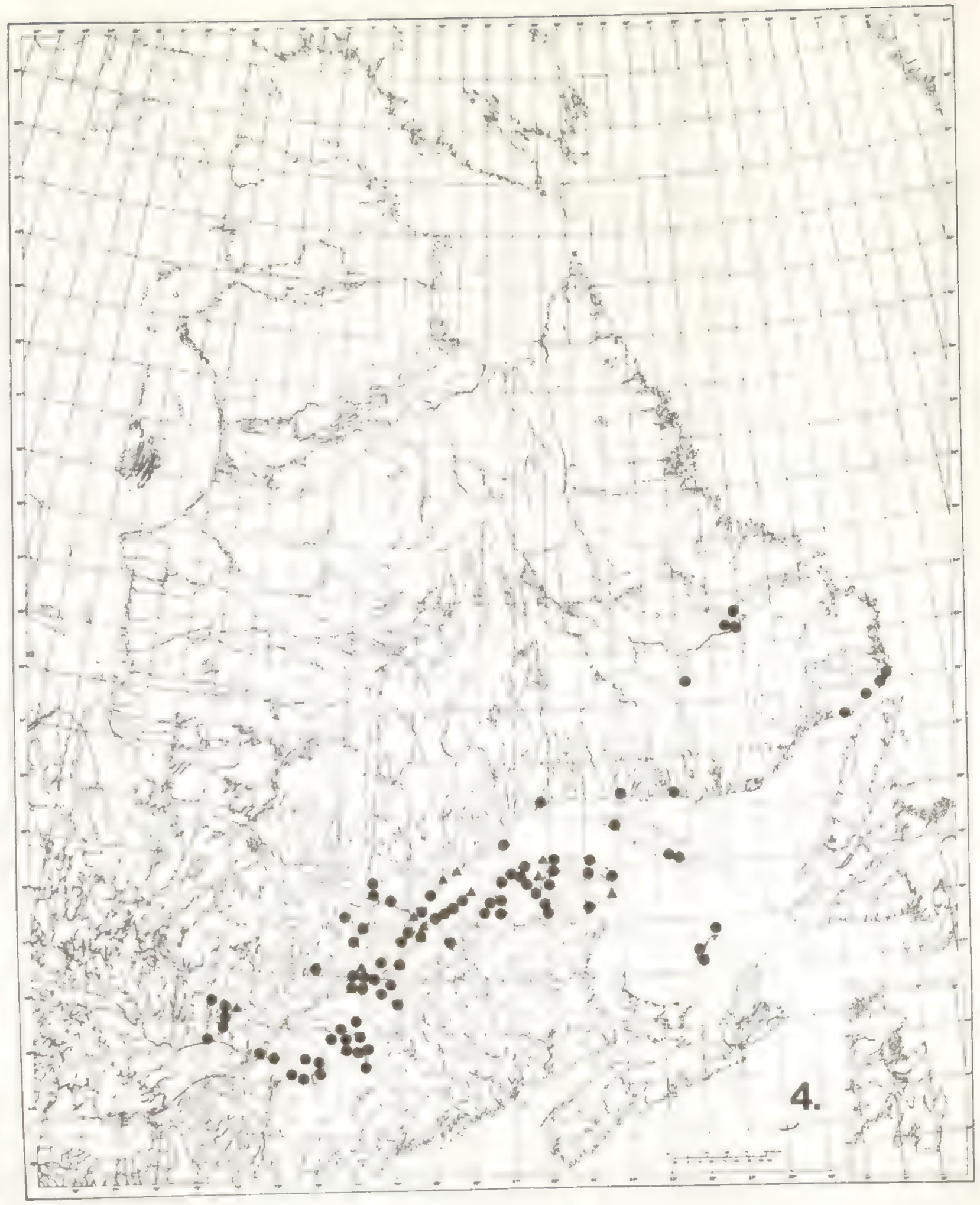
Dryopteris assimilis.—This species (*Fig. 2*) is a northern plant of cool, moist locations. It is well known in Iceland and Greenland and it is the only species of *Dryopteris* found in northern Labrador and Ungava. The known southern limit in Quebec is in La Verendrye Park near Dorval in the west and at the mouth of the Saguenay River, Méits, and Mt. Albert in eastern Quebec. A question that is unanswered at present in whether this species may become an arctic-alpine or sub-alpine in southern Quebec and New England. We have no cytological vouchers from such stations. Although it is unreported from Newfoundland, specimens from the north at St. Anthony would appear to be this species. None of the pteridophytes in Rousseau (1974) have quite the same pattern of distribution, although *Lycopodium alpinum* 6, *Woodsia alpina* 68, and *Woodsia glabella* 69 have some similarities.

Dryopteris spinulosa.—This species (*Fig. 3*) appears to grow in a few favorable locations up to 56° N, although cytological specimens have not been studied north of Amos and Guyenne at ca. 48° 30′ N. There are only four localities plotted from north of 52°, and further study may show that these represent poorly developed plants of *D. assimilis*. There are not as many collections of this species as one might expect. Collectors seem to have favored what they considered to be the more uncommon *D. assimilis*, *D. intermedia* and *D. campyloptera*. The distribution patterns most similar to this appear to *Botrychium virginianum* 26, *Onoclea sensibilis* 59 and *Polypodium virginianum* 62, as published by Rousseau (1974).

Dryopteris campyloptera.—This Appalachian species (*Fig. 4*) reaches its northern limit in western Quebec at Mt. Tremblant. It is still very abundant at St. Donat de Montcalm, Lac de l'Orignal in comté Terrebonne, Laurentides Parc north of Quebec City, to Forrestville, Percé in the Gaspé, Prince Edward Island, Cape Breton in Nova Scotia, etc. In other words, it is in the Laurentian Highlands. It is not expected above 47°N in the west or 52°N in the east, although it may occur sporadically along the north shore of the Gulf of St. Lawrence and on Anticosti Island. The species is well known from Newfoundland, but those specimens from north of 51°N are probably *D. assimilis*. Some specimens from around Goose Bay Labrador have been included here, but without cytological verification. When one travels along the north shore of the St. Lawrence, *D. campyloptera* is found at the mouth of the Saguenay intermixed with *D. assimilis*, both species are at Islets à Jeremie, but only *D. assimilis* can be found at Islets à Caribou and Sept Iles. The fern in Rousseau (1974) that has the most similar distribution is *Polystichum braunii* 64, which is a species that is often associated with *D. campyloptera* in rich, moist, deciduous woods.

The origin of Dryopteris campyloptera.—Widén and Britton (1971) suggested that *D. campyloptera* might be an autotetraploid of *D. assimilis* contra to the views of Wagner (1963, 1971). This decision was based on the following evidence: (1) Chromatographic results did not support the suggestion that present day *D. intermedia* was one parent of *D. campyloptera;* (2) A great majority of the specimens studied of *D. campyloptera* were glabrous, whereas hydrids with *D. intermedia* are known to have glandular indusia and midribs; (3) Early genome analysis by Walker (1961) suggested that *D. intermedia* was conspecific with *D. maderen-*





Distribution of *Dryopteris* in Quebec and Labrador. FIG. 3. *D. spinulosa*. FIG. 4. *D. campyloptera*. ▲ = collections cytologically determined.

sis and the latter species had the same ancestral genomes as *D. assimilis;* and (4) The analysis of pairing in hybrids of *D. assimilis* × *campyloptera* showed more than 41 pairs (46–49) of homologous chromosomes.

We now have the geographic evidence to consider. *Dryopteris assimilis* is a northern species and the derived *D. campyloptera* has a northern limit not unlike that of *D. intermedia*. There is very little overlap between *D. assimilis* and *D. campyloptera*. This evidence favors the view that *D. campyloptera* is indeed a derived allotetraploid of *D. intermedia* and *D. assimilis*. Wagner (pers. comm.) has pointed out that studies on spore sizes (Britton, 1968) also suggest that one parent of *D. campyloptera* should have small spores, e.g., *D. intermedia*, since *D. assimilis* and *D. campyloptera* have overlapping ranges of spore sizes. In the northern part of the range of *D. campyloptera* there are great difficulties in separating this species from *D. assimilis* unless one has cytological as well as morphological evidence. Also, the two species hybridize with each other more readily than with any other *Dryopteris* species. Their phenotypic similarity suggests that their genotypes must be very similar. In order to separate *D. campyloptera* from *D. assimilis*, one must find the very small contribution in *D. campyloptera* from a parent such as *D. intermedia*: more finely cut leaf, some evidence of firmer leaf texture and subevergreen leaves, some darker stipe scales, some influence on the shape of the basal pinnae, a more upright form, etc. These are all characters which are difficult to quantify and equally difficult to reduce to a simple, reliable key.

Dryopteris assimilis in Ontario.—The only major additions to the distribution map for *D. assimilis* (as *D. dilatata*) given by Britton and Soper (1966) are Reznicek's collection at Moosonee and Riley's collection in the Cochrane District at the latitude of Amos in Quebec. These two collections are connecting links with the collections of *D. assimilis* on the eastern side of James Bay (*Fig. 2*), and remove this species from one found only in the Lake Superior basin of Ontario.

In 1934, Dr. Wherry collected a specimen (TRT Acc. No. 118558) from Beaver Pond in Algonquin Park. He kindly gave me the exact location for this collection, which he said was unfortunately near the edge of the lake where there would be a good deal of ice movement in the spring. Several prolonged searches in the immediate area of this collection have failed to produce any living plants for cytology. Algonquin Park is noted for the presence of plants such as *Saxifraga aizoon* and *Lycopodium selago* with northern affinities, as well as plants such as *Picea rubens* with Appalachian affinities. Accordingly, this collection of Dr. Wherry could belong to either *D. assimilis* or *D. campyloptera*; however, its location in the more mesic hardwoods would suggest that it be referred to *D. campyloptera*, in which case it is our only specimen for this species in Ontario!

Hybrids.—The only common hybrid in this group is *Dryopteris* × *triploidea* Wherry (*D. intermedia* × *spinulosa*). One can usually find this hybrid wherever *D. intermedia* and *D. spinulosa* grow together. A distribution map for this species should be very similar to that for *D. intermedia* (*Fig. 1*). The only other hybrid involving just these four species of the *Dryopteris spinulosa* complex that has been collected in Quebec is *D. assimilis* × *campyloptera*, from near Mt. Albert

(Widén & Britton, 1971). It should be stressed that the morphological variation that one finds in these four species can *not* be attributed to the occurrence of hybrids. A concerted effort was made to find hybrids of *D. intermedia* × *campyloptera*, *D. campyloptera* × *spinulosa*, *D. assimilis* × *intermedia* and *D. assimilis* × *spinulosa*, and none were found. They must be of rare occurrence (Widén et al., 1975).

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Ferns: Potential In-situ Bioassay Systems for Aquatic-borne Mutagens

EDWARD J. KLEKOWSKI, JR. and DAVID M. POPPEL*,[1]

It is now apparent that cancer constitutes one of the leading health problems in the United States. A major investment of the energies and resources of the scientific community is being made to understand something of the causes of cancer as well as its cures. Parallel, and in many cases included, with these studies are investigations into the mechanisms of mutation of the genetic material (DNA), which, given the heritable nature of the cancerous state in a given cell line, may shed light on the mechanism of cancer induction and growth (Freese, 1971).

Equally apparent in recent years is the increasing introduction of man-made chemicals into our environment, either by their disposal in industrial wastes or via their use in pesticides, plastics, food additives, drugs, etc. Environmental groups raise a cry of warning against these pollutants, while biochemists show that an increasing number of the chemicals now present in our soil, air, water, food, and manufactured products are chemical carcinogens and mutagens. The debate has thus begun as to the benefits and risks of using such chemicals. But in order for the crucial debate to be meaningful, much precise information must be collected. Various methods are needed to assay the impact of technology on biology, both in the laboratory and in the field, using rapid microbial systems, critical mammalian systems, and on-site monitoring of native plant and animal populations.

Plant geneticists and cytogeneticists can contribute their study of mutations to the problems of cancer and environmental carcinogenesis. The value to cancer research and cancer prevention of studying mutations and mutagens has been demonstrated in recent years by the significant correlation between the cancer-inducing properties of various chemicals and their capacity to induce mutations in DNA in a wide variety of organisms (Miller & Miller, 1971; Ames et al., 1973, 1975). To quote from the Millers' survey: "In summary, it appears that many, perhaps all, chemical carcinogens are potential mutagens. Similarly, many, but possibly not all, mutagens are potential carcinogens." Test systems used to establish these correlations have utilized organisms ranging from viruses, bacteria, fungi, angiosperms, and fruit flies to mammals; even extracts from mammalian tissue are tested in the more practical and efficient bacterial systems. A wide survey of carcinogens, many of them known human carcinogens, in one such bacterial system found that 90% (156/174) of carcinogens tested are also mutagenic (McCann, et al., 1975).

The presence and activity of these and other suspect chemicals in our environment must be detected and analyzed. Such screening and subsequent elimination from the environment may provide the major means of cancer prevention. We are allowing ourselves to be exposed increasingly to chemical carcinogens and muta-

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gens that are being more strongly implicated as factors initiating most human cancer (Cairns, 1975; Epstein, 1974; Higginson, 1969). Cairns (1975) said that "a substantial proportion of cancer deaths could be prevented by controlling appropriate constituents of the environment." The problem then, to a great extent, becomes one of characterizing mutagens/carcinogens and detecting their presence and activity in the environment. The screening of entire ecosystems for the presence of mutagens may become a tractable problem if the appropriate bioassay systems are available. One method of approaching this problem is to measure mutation rates in some component of the flora of a given ecosystem. For example, the detection of increased mutation rates in certain species of an aquatic ecosystem which is characterized by the presence of certain kinds of industrial pollution certainly would warrant further laboratory testing of the pollutants for mutagenic activity. The value of in-situ plant bioassay systems for mutagens in these situations is that such bioassays serve as continuous and cumulative monitors, and so long periods of time are screened. Samples of water or undiluted effluent will vary in their mutagenicity since given mutagens resulting from industrial pollution vary as industrial production and methods change during the course of time. In contrast, the mutations of a submersed or semi-submersed plant species in a riparian ecosystem should reflect the cumulative genetic damage that has occurred during a long period of time. This period of time may be a single growing season or many years, depending upon the plant. In some bioassays it may be possible even to date when mutation rates changed; this refinement requires a detailed knowledge of the organography and ontogeny of the plants. This paper discusses a fern bioassay system with which a riparian ecosystem was screened for mutagenic activity and an attempt made at dating the mutational events.

For the past seven years, the senior author has been developing experimental techniques for the detection of genetic variability in fern populations (Klekowski, 1970, 1973). Recently these techniques have been applied to fern populations growing in environments that are polluted heavily with industrial wastes (Klekowski, 1975, 1976; Klekowski & Berger, 1976). These techniques, based on the Royal Fern, *Osmunda regalis* var. *spectabilis* (Willd.) Gray, involve the detection of both gene and chromosome mutations and whether such mutations have been induced post-zygotically in the parental sporophyte. The Royal Fern is admirably suitable for storing environmentally induced mutations. It has rhizome apices and leaf primordia based upon single apical cells that divide and give rise to all subsequent cells of a given organ. The induction of a mutation in these apical cells results in the mutation being passed to all subsequent cells of the organ. Therefore, as long as the mutations are not dominant cell lethals, they would be expected to accumulate in the genotypes of those organs as the organism grows and as mutations occur. Dominant deleterious mutations, involving those loci which control meiosis and aspects of early embryogeny, as well as recessive and dominant mutations at those loci involved in spore development, gametophyte maturation, gametangia development, zygotic development, and early embryogeny may be expected to accumulate in the apical cells of these organisms. Techniques are available to screen the genotype of a sporophyte for just such

mutations (Klekowski, 1971). Spore samples obtained from single sporophylls of a given sporophyte can be used to generate cultures of gametophytes in the laboratory. The frequency of viable and inviable spores can be scored readily. The gametophytes can be scored for normal and abnormal morphology, and the former used in genetic experiments to determine whether their genotypes contain recessive or dominant zygotic or sporophytic lethals. Techniques to do this involve the establishment of cultures which have one gametophyte each. Such gametophytes become hermaphroditic, forming both antheridia and archegonia simultaneously, and self-fertilization results in formation of homozygous zygotes from which homozygous sporophytes develop. Such sporophytes can be scored for normal or abnormal development.

Meiotic samples taken from the same sporophytes can be screened for chromosome mutations. It is fortunate that in *O. regalis* var. *spectabilis* very large chromosomes are present at meiosis in spite of the fact that $2n=44$. Two types of chromosome aberrations can be detected readily, both of which require two chromosome breaks for their origin. Reciprocal translocations can be detected at meiosis by the presence of multivalents (associations of four chromosomes at metaphase I or trivalents and univalents). It is the latter configuration which is detected most easily as the univalents very often fail to align in the metaphase I plate and with subsequent divisions of meiosis are left in the cytoplasm as micronuclei. Thus a given meiotic sample can be screened readily for the presence or absence of these micronuclei. Where micronuclei occur, further investigation of metaphase I and the pre-metaphase I stages of meiosis reveals the presence of multivalents. Another chromosome mutation that can be screened for in the meiocytes of this fern is the presence of paracentric inversions. Such chromosome mutations result in the formation of bridges and acentric fragments at anaphase I or anaphase II of meiosis. The occurrence of these configurations is based upon the position of cross-overs in the bivalent containing the inverted segment. The presence of bridges and acentric fragments in a sample of meiocytes can be taken as evidence of inversion heterozygosity (see Klekowski and Berger, 1976, for further discussion on the detection of chromosome aberrations in ferns).

In New England the Royal Fern is found commonly in most moist habitats, swamps, and bogs, and very often occurs as a component of the riparian flora. In the latter cases, the fern grows at the edges of watercourses, and very often its rhizomes are submersed periodically. The fern occurs only in rivers where silting is not a normal situation. The Royal Fern population which we investigated grows along the Millers River below Erving, Massachusetts.

The Millers River, a tributary of the Connecticut River, is approximately 50 miles long and drains 300 square miles of north central Massachusetts and 70 square miles of southern New Hampshire. Along its length the quality of the mainstem and its tributary the Otter River varies and is classified from B (good) to D (poor) based on a scale of the Massachusetts Division of Water Pollution Control. The 1.5 mile portion in which the *Osmunda* population grows is classified currently as D. The population consists of approximately 100 plants along the south bank of the river one mile below the outfall of the Erving Paper Com-

pany, Inc. Many of the plants have their rhizomes and shoot apices submersed most of the year. Fronds are initiated below the surface and emerge from the water as the fiddleheads uncoil. Only submersed plants were studied genetically.

Meiotic samples collected in the spring of 1973 from the Millers River population revealed that approximately 43% were heterozygous for chromosome mutations such as paracentric inversions and reciprocal translocations, whereas less than 1% of meiotic samples collected from nearby, non-polluted control populations gave evidence of such mutational heterozygosity. These control populations were taken from areas within the Millers River watershed.

Further analysis of the chromosome mutations present in the Millers River population was undertaken in the spring of 1974. Meiotic collections were made to determine the nature of the cytogenetic chimeras present within the sporophytes. The patterns of chromosome mutations were analyzed in an effort to date the time of induction. After extensive analysis, it was found that practically all the chromosome mutations detected in 1973 and 1974 represented mutations that had occurred since the sporophytes were growing in the Millers River, i.e. were post-zygotic mutations. It was found also that 64% of these chromosome mutations were induced since 1969. Thus, it was concluded that the waters of the Millers River were active mutagenically.

The frequency of Royal Fern sporophytes which are chimeric for gametophytic and sporophytic lethals also was studied in both the Millers River and control populations. A hybridization program was designed to determine whether the several interconnected rhizome apices resulting from the continued growth of a single sporophyte were heterozygous for allelic lethals (for details see Klekowski, 1976). Where the genotypes of these apices differed with reference to these lethals, post-zygotic mutations have occurred. Approximately 40% of the sporophytes studied from the Millers River population were chimeric for such deleterious mutants, whereas chimeras were absent from the control population in the non-polluted environment. This value (40%) is remarkably similar to the frequency of sporophytes exhibiting chromosome mutations (43%) based upon the cytological investigation previously discussed. The similarity of the genetic and cytological studies suggests that both methodologies give useful estimates of the amount of post-zygotic mutational damage present in the population. Because of the laborious and expensive nature of the genetic investigations (due to the prolonged culture and maintenance of thousands of gametophyte cultures), it appears that cytological methods offer an easier method of detecting post-zygotic mutational damage in Royal Fern populations.

These studies of the Royal Fern suggest that other ferns growing in riparian situations may be useful for in-situ bioassay systems of water-borne mutagens resulting from industrial pollution. Species such as *Lorinseria areolata* (L.) Presl, *Matteuccia struthiopteris* (L.) Tod., *Onoclea sensibilis* L., and members of the genus *Acrostichum* have the appropriate ecologies. But whether these species have the appropriate sensitivity, as well as suitable cytological and cultural characteristics, must be investigated before their usefulness for mutagen bioassays can be determined.

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REVIEW

"FERN GROWERS MANUAL," by Barbara Joe Hoshizaki. xi + 256 + xiii pp. 1976. Published by Alfred A. Knopf, Inc. $15.00.—This manual is the best book on fern horticulture on the market at present. It is an instant classic, and is bound to be *the* reference on fern horticulture for the next decade. Barbara Joe Hoshizaki, in words, but best of all in pictures and diagrams, tells realistically how to grow and propagate many diverse true ferns, as well as the lower vascular plants like *Equisetum*, *Lycopodium* and *Selaginella*. This book goes beyond general statements (like not burying the crown when transplanting) to explain exactly how to repot ferns with long creeping rhizomes, those with erect, stocky crowns, or those sometimes difficult Staghorn ferns, which grow on plaques like the picture-frame plants that they are. This book should adequately answer most growers' questions on fern horticulture, with chapters on soils and fertilizers, year around needs, landscaping with ferns, and growing special ferns like the Maidenhair and desert ferns. A long chapter named "Troubles" is probably the best treatment in print of fern pests and the appropriate remedies.

The "Manual" is a technical book about a specific subject, yet it is written in non-technical terms. There is a glossary to guide the amateur reader, and three useful appendices are included to help the grower. These tell how to measure light intensity, how to find information and supplies from lists of commercial suppliers, and how to locate the world's prominent fern societies.

The simple and direct style makes this book a pleasure to read. It is a little shy in literature citations, especially taxonomic citations to specific names. This makes it difficult for the reader to find the original taxonomic sources. A number of nomenclatural problems are straightened out, like the disparity between botanical names of Tree Ferns and the names used in the commercial trade. The names presented in this volume give us a reliable list of the ferns currently in cultivation in the United States.

Very few good, reliable sources of information on fern horticulture are available. This book provides extremely knowledgeable directions on how to grow ferns in the home, the greenhouse, or outdoors. The author has overcome the regional bias shown by many horticultural writers; her book has universal relevance.

It would have been helpful if all the species and varieties mentioned in the list of 480 plants were pictured because many cultivars are hard to characterize in written descriptions. But pictures of everything are impossible in a book of this scope. However, an especially useful system of code-words gives a concise and quick key to the structure and cultural requirements for every species listed. The inclusion of common and uncommon, easy and difficult varieties in the trade and in cultivation gives the fern gardener a list of possible plants to add to his collection. For everyone interested in growing ferns this book is an indispensable aid. The informative text, 240 photographs (15 in color), and 57 diagrams make this book a real bargain.—*Bruce W. McAlpin, New York Botanical Garden, Bronx, NY 10458.*

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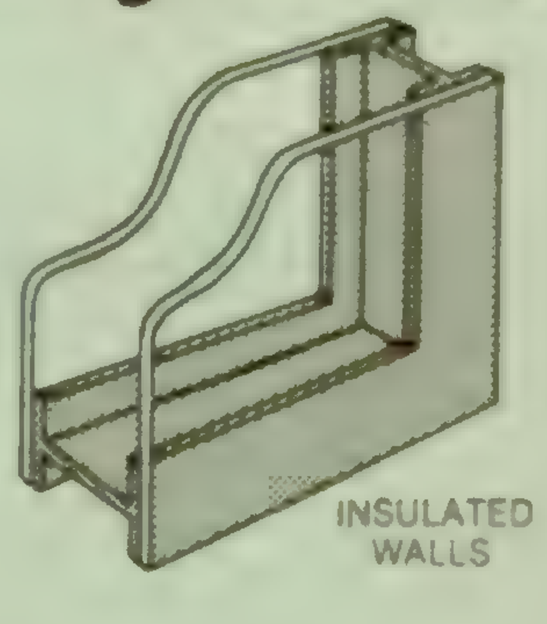

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Vegetative Propagation in Asplenium exiguum

JOHN T. MICKEL*, [1]

Asplenium is one of the largest, most diverse, and widespread genera of modern ferns. Many of its nearly 800 species reproduce vegetatively by buds. In different species or species groups, buds have been reported on the roots (*A. auritum*, *A. cuspidatum*), in the axils of basal pinnae (*A. monanthes* var.), in the axils of several pinnae (*A. commutatum*), on the rachis near the apex (*A. sessilifolium*, *A. polyphyllum*), on an attenuated rachis tip (*A. radicans*, *A. rutaceum*, *A. rhizophyllum*), and plantlets have been observed on the upper surface of the pinnae (*A. bulbiferum*, *A. viviparum*), and on stolonoid fronds (*A. mannii*, *A. bipinnatifidum* complex). See Faden (1973) for a more detailed treatment of buds and plantlets in *Asplenium*. The various means of vegetative reproduction in *A. exiguum* are reported here and its horticultural possibilities are discussed.

Asplenium exiguum is a small spleenwort (fronds 3-20 cm tall) with an interesting disjunct geographic distribution. It is found in the Himalaya Mountains, the Philippine Islands, Mexico, and the southwestern United States. In 1971 the author discovered it in the Mexican state of Oaxaca near the village of Ixtlán de Juárez, growing on dry, exposed rocky cliffs and shaded ravines. Plants growing on the more exposed sites occasionally rooted at the tip of an extended rachis. This mode of reproduction has been noted by Bir and Shukla (1968), Copeland (1960, p. 442) and Knobloch and Correll (1962, p. 151).

Living plants transplanted to the New York Botanical Garden greenhouses have survived well. One plant was placed in our cloud forest chamber (the type described by Farrar, 1968), where it had nearly 100% humidity. After a few months, three methods of vegetative reproduction expressed themselves. A few fronds had prolonged apices with rooting tips (*Fig. 1e*); occasionally a frond forked at the tip (*Fig. 1c*), resulting in two proliferous apices. Some fronds developed buds at the base of pinnae near the tip of the rachis (*Fig. 1e*); this type has not been noted for this species previously. The most unusual development, however, was that a plantlet developed at the apex of many pinnae, forming a necklace of young plants around the entire frond (*Figs. 1b, d*). This is most pronounced on the older fronds as they lie close to the ground. Careful examination shows that all pinnae, whether they are on living plants in the cloud forest chamber or the greenhouse or are on herbarium specimens, bear a bud in the notch at the apex (*Fig. 1a*). Apparently wild plants only rarely get sufficient humidity to allow the buds to produce plantlets, for only rarely on herbarium specimens was it possible to detect with magnification the slightest germination of these buds, and plantlets were never seen.

These pinna proliferations have been noted only once before (Bir & Shukla, 1968), but their illustration (their fig. 27) shows the bud arising on the lower

*The New York Botanical Garden, Bronx, New York 10458.

[1]This work was supported by grant BMS 75-08358 from the National Science Foundation. I am grateful to Mr. Edgar Paulton for preparing the drawings.

surface of the lamina. This is incorrect; in all specimens buds arise in the terminal notch of the pinna.

I know of no other species of *Asplenium* or of other ferns that bear buds at the pinna apices. With sufficiently high humidity, apparently this is a very efficient means of propagation in this species. It is curious, though, that the species is found in habitats that do not permit development of these buds. The fact that it produces buds in three different positions is equally remarkable.

Many species of *Asplenium* have been used in cultivation, and *Asplenium exiguum* may well be added to the list. It seems to be ideally suited for horticultural use in terraria or bottle gardens. It can withstand the very high humidity, it grows rapidly, it remains relatively small, it is an attractive plant in its natural habitat, and it is even more striking with the small plantlets along the frond outline. It is propagated readily by placing the plantlets in soil or on wet peat, and can also be grown well from spores. Hopefully, the number of these plants in cultivation will be increased so this species can be more widely distributed.

FIG. 1. *Asplenium exiguum*. FIG. 1a. Dorsal surface of pinnae with terminal buds. FIG. 1b. Dorsal surface of pinnae with plantlets. FIG. 1c. Forking frond tip. FIG. 1d. Ventral surface of pinnae with plantlets. FIG. 1e. Frond apex with terminal plantlet and rachis bud.

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Cold Requirements of Several Ferns in Southeastern Michigan

ROYCE H. HILL*,[1]

Dormancy mechanisms constitute a major adaptation of plants in the colder temperate zones. Dormant organs are especially resistant to winter cold, and it is known that an annual cold period is not only tolerated but is actually required for the resumption of growth in some temperate zone species. A cold requirement for completion of the annual cycle of growth and development in flowering plants native to the temperate zones is well known (Salisbury & Ross, 1969). However, little or no information is available on the role of low winter temperatures in the life cycle of temperate zone ferns.

Preliminary experiments suggested that six local fern species differed widely in their dependence on a cold treatment for renewed growth. Three species (*Osmunda claytoniana* L., *Athyrium filix-femina* (L.) Roth, and *Matteuccia struthiopteris* (L.) Todaro) required at least 30 days of outdoors cold treatment, during November-February, to produce appreciable bud-break indoors. The other species (*Cystopteris fragilis* (L.) Bernh., *Adiantum pedatum* L. and *Thelypteris palustris* Schott) broke bud after a cold period of only 12 days.

PROCEDURE

Plants of seven species of ferns were collected from their natural habitats during September 23-30, 1970. Fronds of these were cut back to ground level and the rhizomes, including buds, were potted in a soil mixture containing equal parts of sand, loam, and leaf mold. The plants were divided into six groups of ten plants each. The untreated group was placed in the greenhouse immediately after collection. The 12-week cold treatment group was placed in a cold room (a refrigerated storage room kept at 5°C and darkness) immediately after collection for 12 weeks.

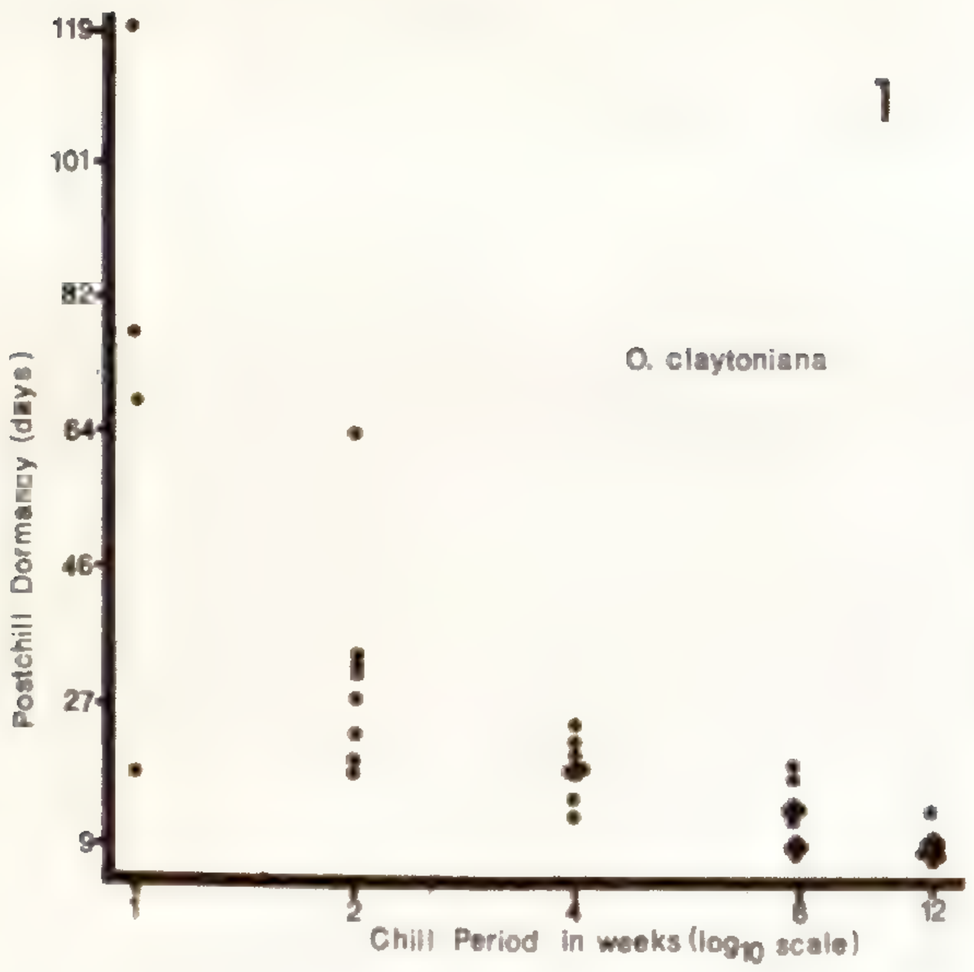
The other four groups were placed in a holding room at 15°C and 8-hour photoperiod for varying periods of time before being placed in the cold room, resulting in different periods of cold treatment. For example, the 8-week treatment group was placed in the holding room for four weeks and then the cold room for eight weeks. With this experimental design, it was possible to remove all groups receiving cold treatment to the greenhouse at the same time. None of the rhizomes broke bud in the holding room, and the cool temperature (15°C) probably was not sufficiently low to satisfy cold requirements of the plants; generally, temperatures effective in breaking dormancy in buds are those below 10°C (Salisbury & Ross, 1969).

The groups receiving cold treatment were brought into the greenhouse on December 28. Greenhouse temperatures were 20-30°C during the day and 15-25°C at night. Photoperiods were effectively 24 hours, as incandescent lights illuminated the plants continuously.

---

*Science Department, Huron High School, Ann Arbor, MI 48105.

[1]I wish to acknowledge the guidance of Dr. Warren H. Wagner, Jr. and Dr. Edward L. McWilliams and the use of the facilities of the Matthaei Botanical Gardens, University of Michigan.


1
O. claytoniana
Postchill Dormancy (days)
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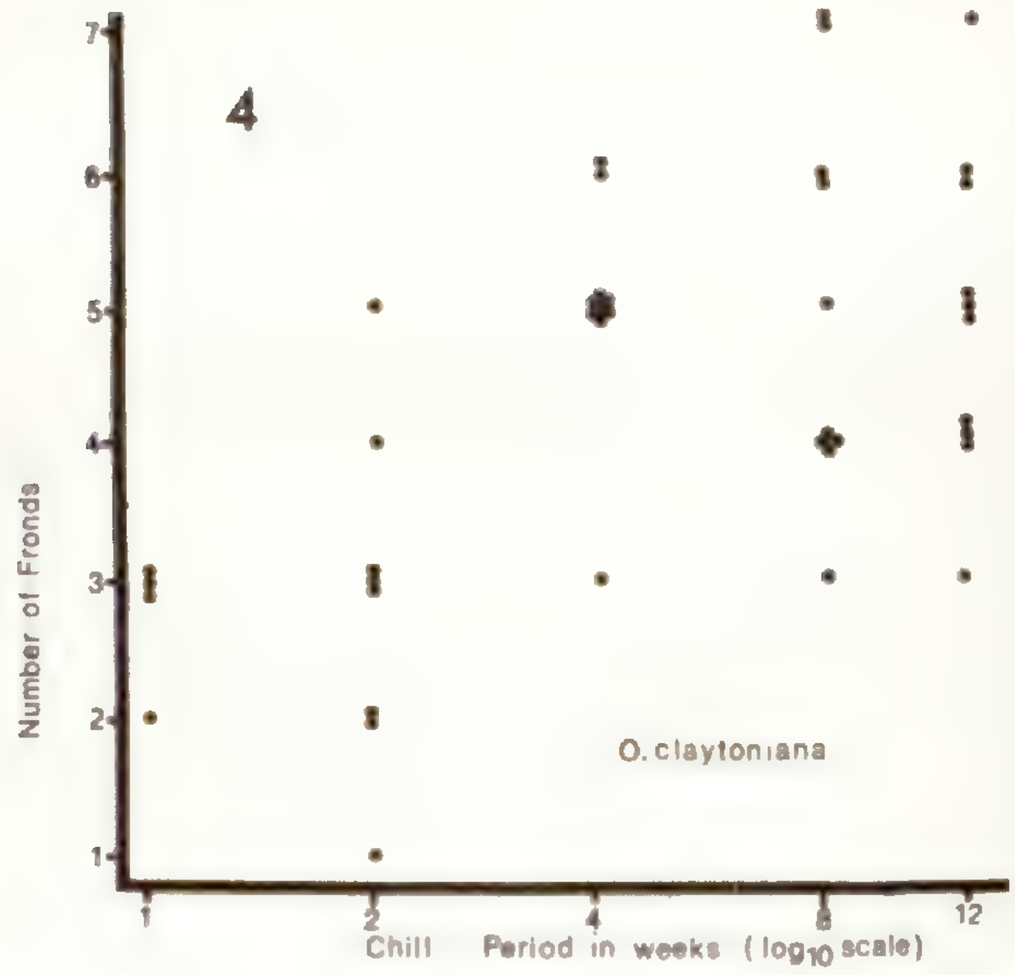
4
O. claytoniana
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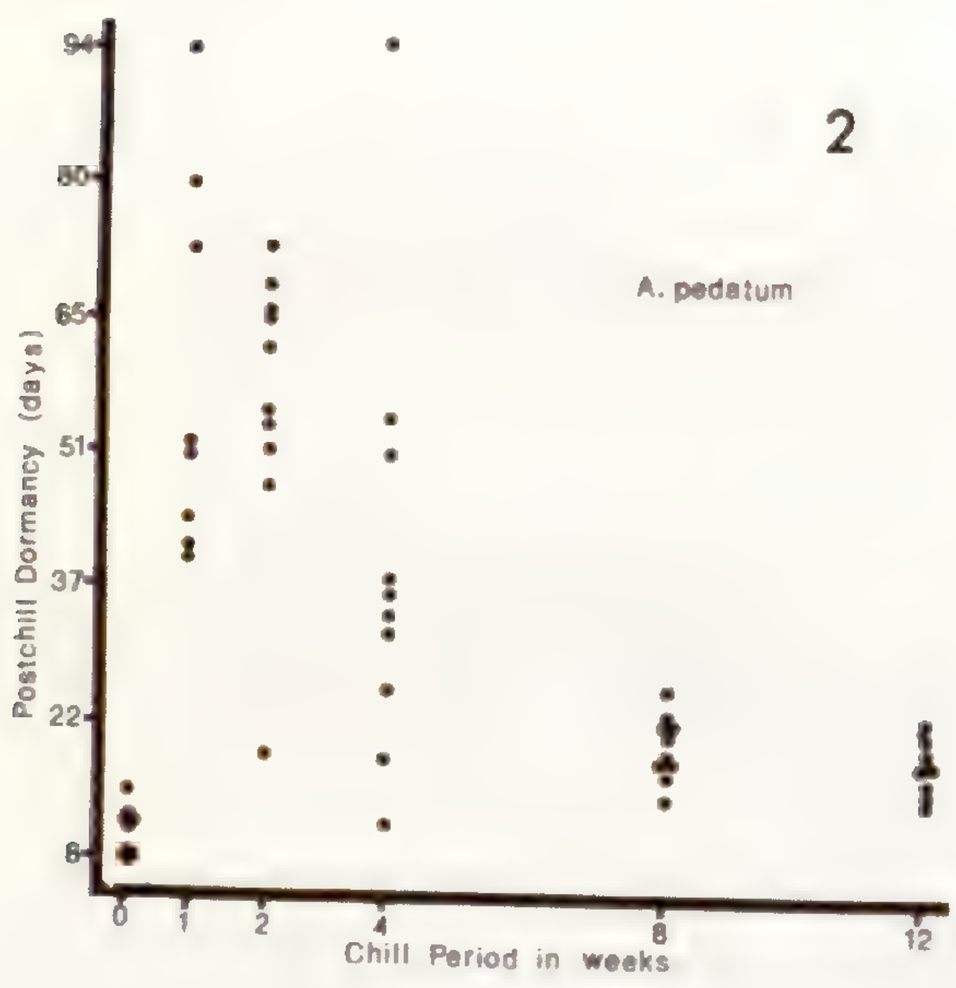
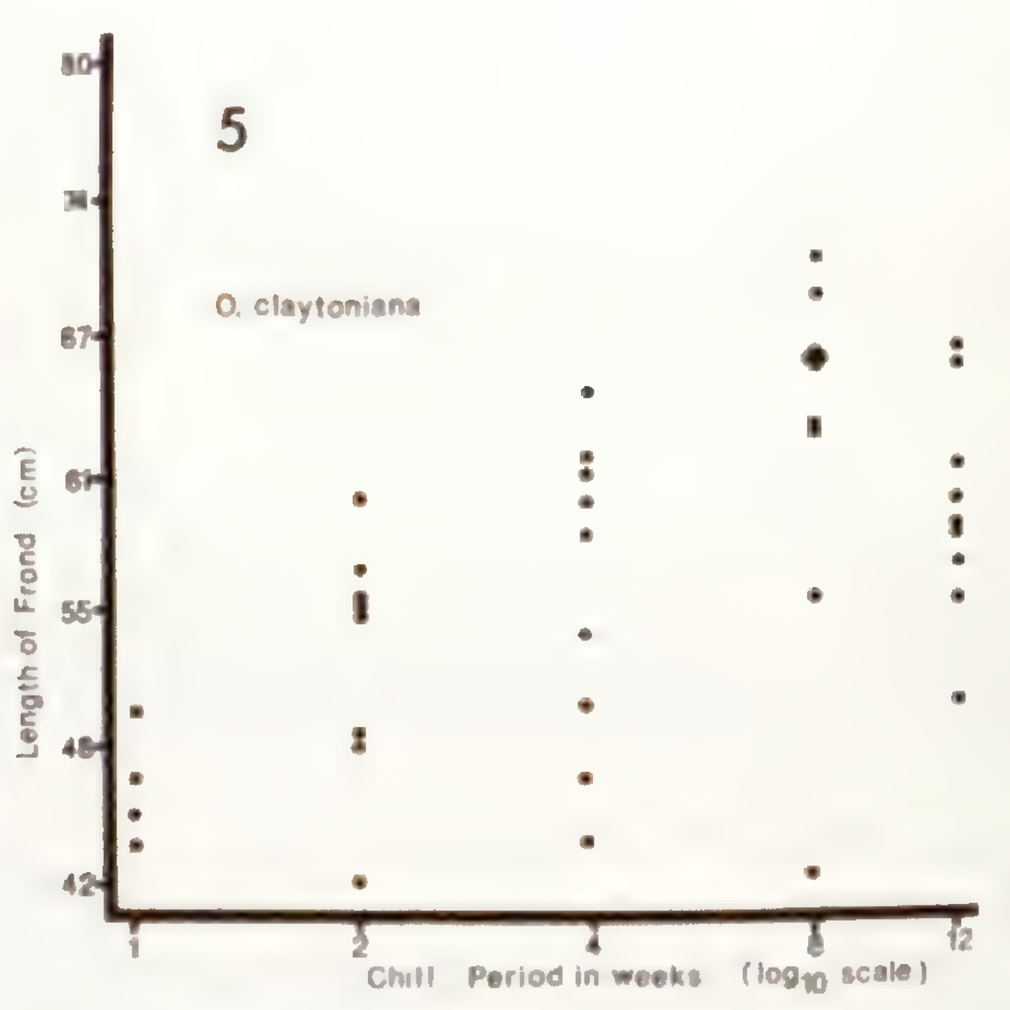
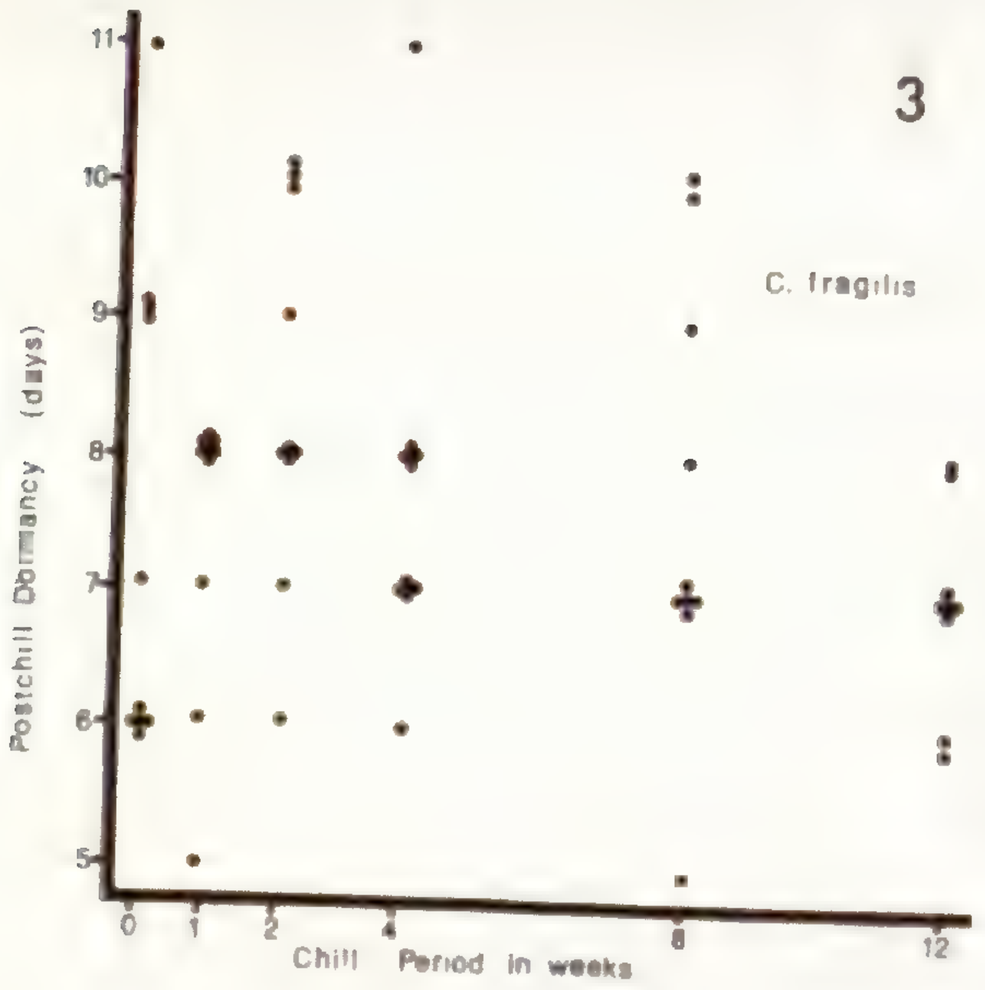
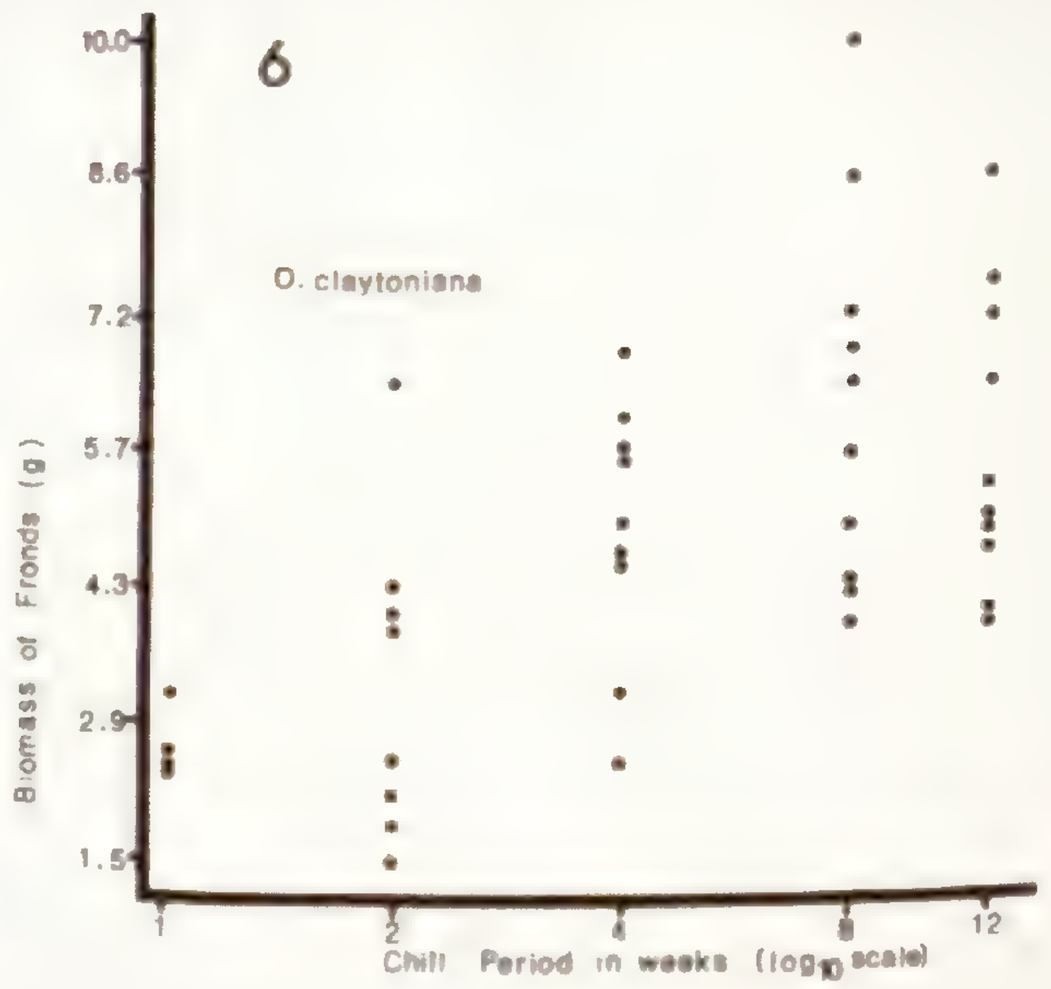
12
Chill Period in weeks (log10 scale)


2
A. pedatum
Postchill Dormancy (days)
94
80
65
51
37
22
8
0
1
2
4
8
12
Chill Period in weeks


5
O. claytoniana
Length of Frond (cm)
80
74
67
61
55
48
42
1
2
4
8
12
Chill Period in weeks (log10 scale)


3
C. fragilis
Postchill Dormancy (days)
11
10
9
8
7
6
5
0
1
2
4
8
12
Chill Period in weeks


6
O. claytoniana
Biomass of Fronds (g)
10.0
8.6
7.2
5.7
4.3
2.9
1.5
1
2
4
8
12
Chill Period in weeks (log10 scale)

The date of bud-break was recorded for each plant, and growth measurements were taken 60 days later. These measurements included the number of fronds per plant, length of the longest frond per plant, and oven-dry weight (biomass) of the fronds per plant. Percentage-soriation (the percentage of fronds that were fertile for each group) was recorded for each treatment.

RESULTS AND DISCUSSION

Since the untreated group of each species was taken directly from the field to the greenhouse, it was possible to determine whether the plants were dormant at the time of collection in late September. Untreated plants of all species except *Osmunda claytoniana* L. broke bud at high percentages shortly after being brought into the greenhouse.

The percentage of bud-break in *Osmunda claytoniana* increased with increasing cold period, from 40% after one week of cold treatment to 100% after 8–12 weeks of cold. Postchill dormancy, the time lag between the events of removing the plant into the greenhouse from the cold room and the indoor bud-break of the plant, decreased markedly with increasing length of cold treatment periods. Duration of postchill dormancy decreased from as long as 120 days after one week of cold treatment to about 10 days after 12 weeks of cold treatment (*Fig. 1*). In total time before bud-break (cold treatment period plus postchill dormancy period in the greenhouse), plants treated for only one week required 127 days to break dormancy, whereas those treated with a cold period of 12 weeks required 94 days to break dormancy. Thus, longer cold treatments up to 12 weeks decreased the overall length of time until bud-break by about 33 days.

The combined requirements of a cold treatment and a variable postchill dormancy period for bud-break seem to be of adaptive value to this species. Fall-hardened plants would be unable to break bud during unseasonably warm autumn weather. Plants that received only a short cold period by this time either would not break bud or would require a period of postchill dormancy much longer than normally occurs in autumn. Unseasonably warm weather in February or early March would usually be shorter in duration and probably would not provide sufficient hours of temperatures suitable for postchill dormancy and bud-break.

It was impossible to determine the role of photoperiod in controlling bud-break in these experiments, as the plants were placed under 24-hour photoperiods in the greenhouse. In the case of *Osmunda claytoniana,* however, an additional experiment indicated that light has no effect on breaking dormancy. Extra plants of this species were removed from the cold room after four weeks of cold treatment (and darkness), and then were placed in darkness in the greenhouse. All of these plants broke bud. This observation suggests that the breaking of dormancy ultimately is under the influence of temperature.

FIGS. 1-3. The effect of length of cold treatment (chill period) on length of postchill dormancy. The F-value for each regression was significant at P = <.01 for FIGS. 1 and 2. FIG 1. *Osmunda claytoniana*. FIG. 2. *Adiantum pedatum*. FIG. 3. *Cystopteris fragilis*. FIGS. 4-6. The effect of length of cold treatment (chill period) on growth of *Osmunda claytoniana*. The F-value for each regression was significant at P = <.01. FIG. 4. Number of fronds per plant. FIG. 5. Frond length per plant. FIG. 6. Frond biomass.

Kriebel and Wang (1962) found similar cold requirements for Sugar Maple trees native to Michigan. The trees were left outdoors in an Ohio garden and then were brought indoors at intervals during the fall and winter months. The minimum duration of cold treatment promoting bud-break was nine weeks, and long periods of cold treatment resulted in shorter postchill dormancy periods.

Untreated plants of the other fern species studied broke bud and periods of postchill dormancy were shorter in some of the species after receiving no cold

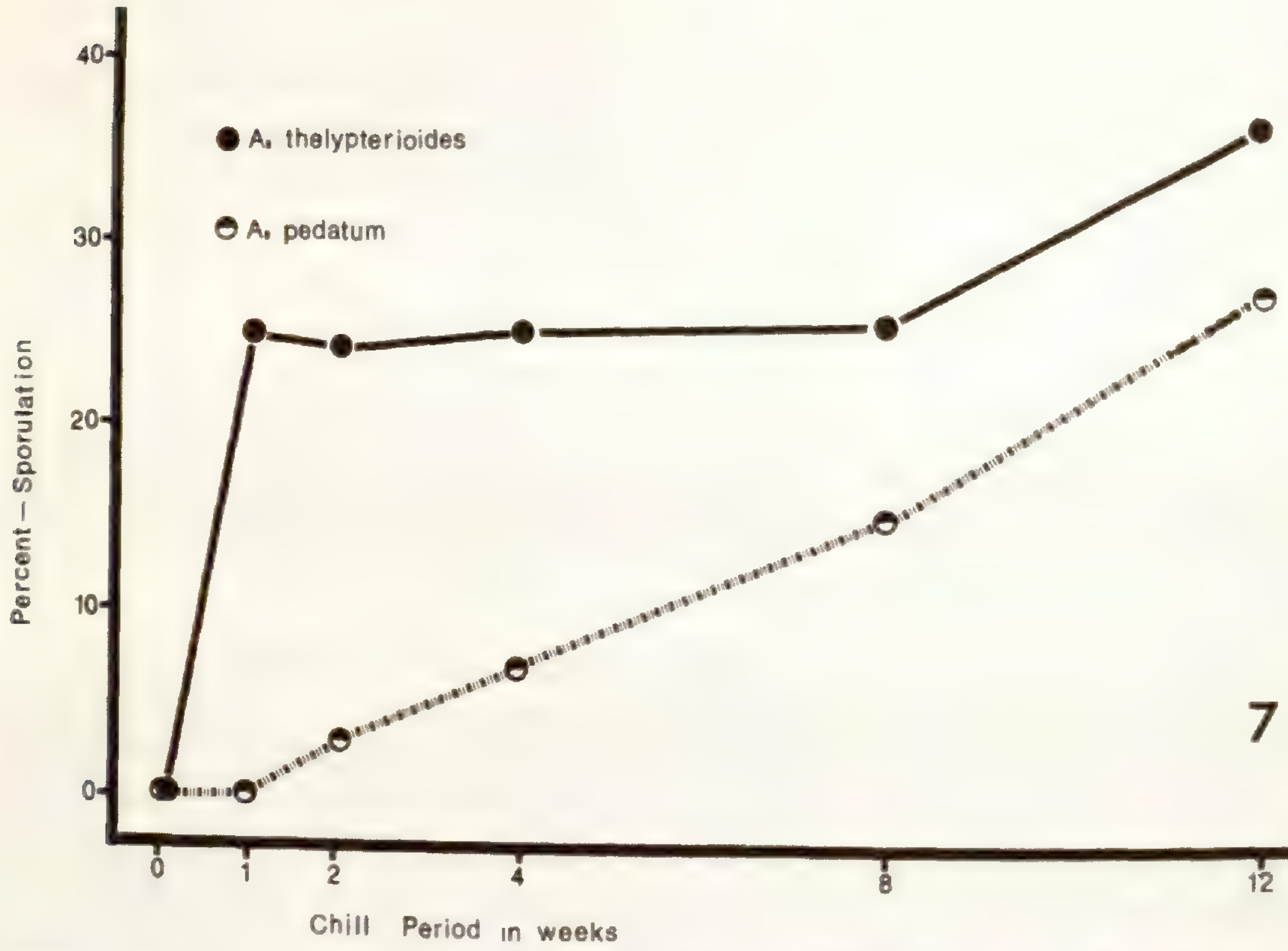


FIG. 7. The effect of length of cold treatment (chill period) on percentage-sporulation of *Adiantum pedatum* and *Athyrium thelypterioides*.

treatment than after receiving one week of treatment. This indicates that the plants were not dormant at the time of collection and that one week at 5°C was sufficient to induce dormancy. This was especially apparent for *Adiantum pedatum* (*Fig. 2*), which had a postchill dormancy of 7–15 days with no cold treatment and 40–94 days after one week of cold treatment. Among treated groups of this species, postchill dormancy periods decreased with increasing length of cold treatment in a manner similar to that observed in *Osmunda claytoniana*. Plants of *Adiantum pedatum* were not dormant by late September, but only one week of cold treatment at 5°C induced a condition of dormancy that was broken only after long periods of postchill dormancy or longer periods of cold treatment. It is apparent that the cool weather following the date of collection would have

been sufficient to cause the plants to become dormant soon in their natural habitats. Dependence of bud-break and duration of postchill dormancy on the length of cold treatment in *Thelypteris palustris* was similar to that in *Adiantum pedatum*, although periods of postchill dormancy in the former never exceeded 26 days in any of the treatments.

High percentages of bud-break and short periods of postchill dormancy in all treatments typified the other four species studied. *Figure 3* shows that postchill dormancy periods never exceeded 11 days in any of the plants of *Cystopteris fragilis*. This indicates that these plants were never dormant, but had remained in a quiescent state during cold treatment. It is likely that these plants merely tolerate low temperatures during the winter months and begin bud-break shortly after the return of favorable temperatures for growth in the spring.

Length of cold treatment appeared to exert especially strong effects on the growth of *Osmunda claytoniana*. The number of fronds per plant increased with increasing length of cold treatment, up to eight weeks (*Fig. 4*). This relationship between frond production and cold treatment was not apparent in the other species studied. Cold-treated plants of *Athyrium thelypterioides* produced more fronds than untreated plants, but increasing the period of cold treatment failed to increase the frond number further.

Frond length and frond biomass also increased with length of cold treatment up to eight weeks in *Osmunda claytoniana* (*Figs. 5* and *6*). Frond length and biomass were higher in cold-treated plants of *Thelypteris palustris* than in untreated plants, but increasing the period of cold treatment did not promote greater frond length or biomass.

Dependence of soriation on cold treatment was found in only two species (*Fig. 7*). None of the fronds of untreated plants of *Athyrium thelypterioides* were fertile, but 25-40% of the fronds of cold-treated plants produced sori. Plants of *Adiantum pedatum* receiving no treatment or one week of cold treatment were infertile, but percent-sporulation increased markedly with further cold treatment.

CONCLUSIONS

It is concluded from these experiments that the species studied differ in their dependence on an annual cold treatment. *Osmunda claytoniana* has an obvious cold requirement for bud-break and vegetative growth and appears to enter dormancy earlier in the fall than the other species. This species may be better adapted to winter temperatures than the other species studied. Bud-break and some parameters of growth were influenced by duration of cold treatment in *Adiantum pedatum* and *Thelypteris palustris*.

At the other extreme, *Cystopteris fragilis, Onoclea sensibilis, Athyrium thelypterioides*, and *Athyrium pycnocarpon* do not appear to require cold treatment for renewed growth and do not seem to enter a true state of dormancy. Plants of all treatments of these species commenced growth soon after they were brought into the greenhouse. These species apparently remain in a quiescent condition during winter. Although it would be expected that plants of these species would suffer frost damage following occasional autumn warming trends, I have not observed

this in the field. Apparently these plants tolerate frost (although I have observed frost damage of some of these species after late spring frosts of great severity) or are more dependent on seasonal photoperiods than on seasonal temperatures for timing of bud-break. Additional studies of some of these species are needed to determine the influence of photoperiod on the induction and breaking of dormancy.

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REVIEW

"A TAXONOMIC REVISION OF THE GENUS CNEMIDARIA (CYATHEACEAE)," by Robert G. Stolze. Fieldiana Botany **37:** 1-98. 1974.—The taxonomy of the American members of the family Cyatheaceae has been a source of frustration to botanists for over a hundred years. Only in the past few years has the group received the critical modern study it needed so badly. Tryon has provided us with an excellent treatment of the family in synoptical form. Revisionary work on the component genera has included papers by Gastony, Tryon, Riba, and Windisch. Stolze's revision of the natural group of species maintained as *Cnemidaria* by Tryon is another in this series of excellent systematic treatments. Pteridologists may now look forward to the day when the entire family will be represented in contemporary monographs of this same kind.

A close look at Stolze's revision reveals the quality of the work. The survey of preserved specimens from herbaria has been extensive. Stolze saw nearly 2000 specimens from at least 17 different herbaria, representing plants from the West Indies, Central America, and South America. Experience in the field has also played a major role in the project. Stolze has provided us with a useful guide to the collection of these giant ferns from his experience with sadly incomplete specimens in the herbaria, and happily complete plants in the field. There is a critical review of the morphology of plants in the genus, including work on the unusual anastomosing venation and porate spores. A section on evolution and geography develops the theme of geographic speciation typical of the American Cyatheaceae. The systematic treatment of the species attests to Stolze's careful attention to the elucidation of nomenclature, and the construction of manageable keys. Indices to Latin names and collections complete the study. The text is provided with illustrations in pen and ink by Richard Roesener. Stolze's definitive work on *Cnemidaria* is a useable one—as long as your material is complete!—*David S. Barrington, Pringle Herbarium, Department of Botany, University of Vermont, Burlington, VT 05401.*

Variation in Costa Rican Ophioglossum palmatum and Nomenclature of the Species

LUIS D. GÓMEZ P.*

In establishing the monotypic genus *Cheiroglossa,* Presl (1845, p. 57) segregated *Ophioglossum palmatum* on the following basis: "Differt ab Ophioglosso habitu, reticulo venarum simplici, ortu spicarum plurium e margine frondis, ab Ophiodermate fronde revera stipitata, venulis secundariis intra maculas et ad maculas marginales liberis, spicis pluribus ad basim frondis marginalibus."

Presl (1845, p. 56) also accepted the epiphytic and monotypic genus *Ophioderma* (Blume) Endl., which differs from *Ophioglossum sensu stricto* and from *Cheiroglossa* in having fronds that are narrow, strap-shaped, and entire or rarely forked at the apex, and in the median, basal position of a single or a pair of fertile segments: "Sed Ophioderma ab Ophioglosso revera differt non solum habitu frondis fasciaeformi, sed praesertim venarum maculis simplicibus, venulis liberis nullis, exortu laterali spicae e vena media frondis."

In the "Index Filicum" Christensen recognized neither segregate; Nakai (1925) rejected *Cheiroglossa* as a genus but upheld *Ophioderma;* Clausen (1938, p. 111) considered *Cheiroglossa* and *Ophioderma* to be subgenera of *Ophioglossum;* and Copeland (1947, p. 11) also submerged both into that genus, stating that a number of species are intermediate and link the three genera.

Although there may be no cytological differences (Ninan, 1958), there are a number of morphological and anatomical reasons for separation at the subgeneric level (Chrysler, 1941; Nishida, 1952; Clausen, 1954, pp. 496–498; Maroti, 1965; van Cotthem, 1973).

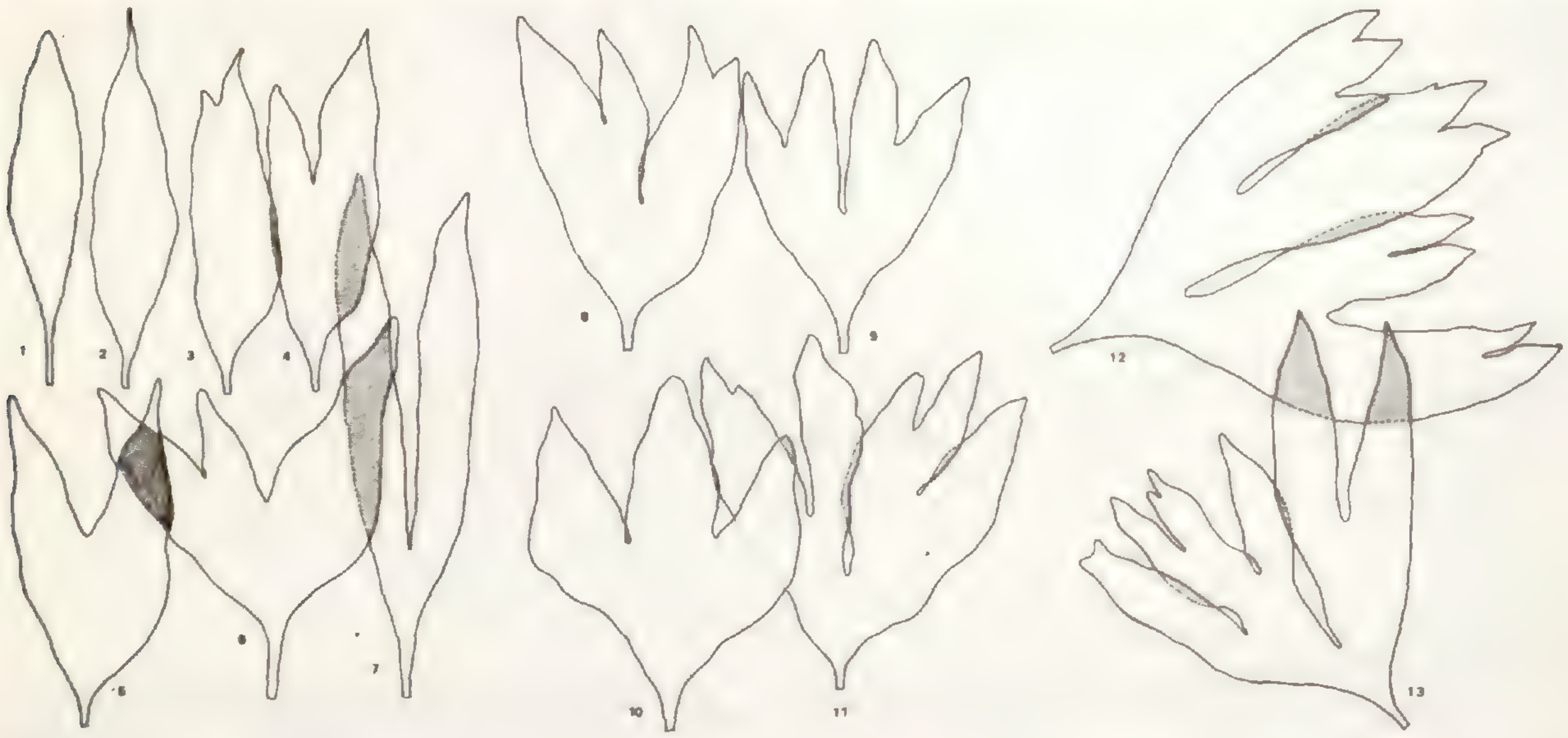
Several species and varieties have been proposed in subg. *Cheiroglossa*. *Cheiroglossa malgassica* (C. Chr.) Pic. Ser., from Madagascar, Réunion, and the Seychelles Islands, differs from typical *O. palmatum* in having smaller fronds and areoles, in the fertile segments mostly inserted near the base of the sterile blade, and in a less deeply incised and thicker lamina and uniformly thick veins. *Cheiroglossa louisii* (Taton) Pic. Ser., from the Congo, has dichotomously segmented fronds with very long, narrow segments, hexagonal, elongate areoles with few included veinlets, and the fertile segments sometimes furcate. Only two collections are known of this species. *Cheiroglossa austrobrasiliensis* Brade, from Brazil, differs in lamina dimensions and color of the sterile segment and common petiole. It has narrow areoles, and the fertile segments are inserted both on the petiole and on the margins of the sterile segment.

The present study is based on six large clumps of *O. palmatum* collected at San Rafael de Vara Blanca, Province of Heredia, at 2000 m altitude. The plants grew as epiphytes on various trees, mostly *Quercus* sp. and *Magnolia poasana* Standl., together with other epiphytes, including Orchidaceae, Bromeliaceae, Araceae, and bryophytes. The area is a montane cloud forest, with rainfall averaging 3000 mm/year and temperatures 18°C. Voucher specimens are: *Wagner & Gómez 1181* (CR), *Lent 1615* (F), and *Gómez 5070* (CR), and totalled 57 fertile fronds.

*Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.

Leaf Shape.—The juvenile leaves of *O. palmatum* are dichotomously lobed from the earliest stages. In cases where the leaf is spathulate with a roundish apex, a median cleft is soon formed. The lamina is very thick, fleshy, and lustrous, and disproportionately short compared to the long, robust petiole.

I have considered as mature and suitable for analysis those leaves which had ripe or dehiscent fertile segments. *Figures 1-3* are simple blades, one of them slightly and irregularly cleft. Such leaves are not common and may be considered as abnormal for the species. *Figures 4, 5, 7,* and *9* depict more or less dichotomously lobed leaves, from slightly cleft to deeply so. *Figures 6* and *8* show irregular, dichotomous forking. *Figure 10* corresponds to a tripartite leaf. *Figures 11-13* are the usual large, old leaves with few to many lobes. Sinuses and segments are not generally alike in a single frond, nor are they uniform within a population.



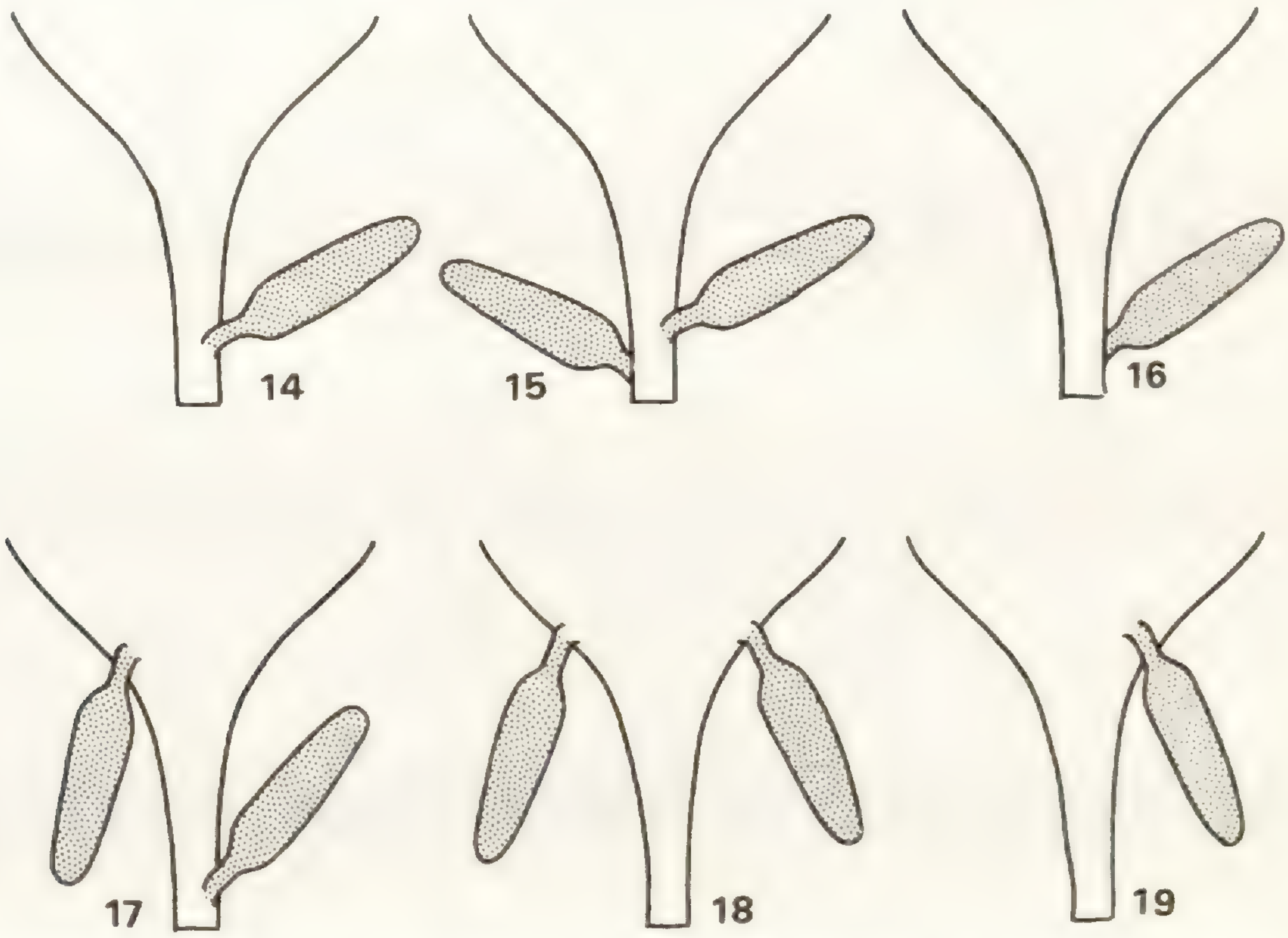
Sterile blades of *Ophioglossum palmatum*. FIGS. 1-3. Simple blades. FIGS. 4, 5, 7 and 9. Regularly dichotomously lobed blades. FIGS. 6, 8. Irregularly dichotomously lobed blades. FIG. 10. Tripartitely lobed blade. FIGS. 11-13. Large, variously lobed blades.

Leaf Size.—The size of mature fronds varies greatly. Length was measured from the base of the blade to the tip of the longest lobe, and is 5-30 cm, with a mean of 17.8 cm. Width, measured transversely at the arithmetic half of the longitudinal axis, is 3.5-24.7 cm, with a mean of 9.3 cm. Apparently there is no constant length/width ratio.

Petioles.—All the petioles examined were terete, glabrous, and slightly furrowed in the area where fertile segments were inserted, due to a low ridge of tissue superimposed on the vascular supply of the fertile segments and their short peduncles. The petioles are 11.5-40 cm long, with a mean of 20 cm.

Fertile Segments.—As a rule the fertile segments are slightly flattened dorsiventrally, obtuse or acutish at the apex, and rounded or truncate at the base. The costa, really a pseudocosta, may be well or poorly defined. The fertile segments are 1.5-6 cm long, with a mean of 4.1 cm, and 0.4-1 cm wide, with a mean of 0.5 cm. The peduncles subtending the fertile segments are 3-12 mm long. The number of marginal pairs of sporangia is 7-41, with a mean of 17.

Fertile Segment Insertion.—The fertile segments of *O. palmatum* are inserted variously on the petiole, the lamina, or both. I have distinguished six types of insertion: (1) adaxial petiolar (*Fig. 14*), with the sporophylls only on the adaxial side of the petiole, in 18 (31.57%) of the fronds; (2) mixed petiolar (*Fig. 15*), with the sterile segments inserted on the adaxial and abaxial sides of the petiole, in 3 (5.26%) of the fronds; (3) abaxial petiolar (*Fig. 16*), with the sterile segments inserted only on the abaxial side of the petiole, in 2 (3.50%) of the fronds; (4) laminar/petiolar (*Fig. 17*), with fertile segments inserted both on the petiole, either adaxially or abaxially, or on the lamina, in 15 (26.31%) of the fronds; (5) marginal laminar (*Fig. 18*), with fertile segments inserted only on the lamina margins, in 9 (15.78%) of the fronds; and (6) superficial laminar (*Fig. 19*), with fertile segments inserted only on the lamina surface, leaving a discernible space between the point of insertion and the margin of the sterile blade, in 4 (7.01%) of the fronds. A mixed condition of superficial and marginal laminar fertile segments was found in one frond (1.33%).



Insertion of fertile segments on *Ophioglossum palmatum* blades. FIG. 14. Adaxial petiolar insertion. FIG. 15. Mixed petiolar insertion. FIG. 16. Abaxial petiolar insertion. FIG. 17. Laminar/petiolar insertion. FIG. 18. Marginal laminar insertion. FIG. 19. Superficial laminar insertion.

Blade Venation.—The areoles formed by the anastomosing veins, which have been used to differentiate some supposed species of *Cheiroglossa*, were found in the material studied to be variable in size and shape, with no constant length/width ratio apparent. They are 8–35 mm long, with a mean of 22.7 mm, and 1.9–7.5 mm wide, with a mean of 3.9 mm. The foregoing measurements are from ten areoles on each blade of the 57 studied, chosen at random along the line used to measure blade length.

One of the distinguishing characters proposed by Presl to differentiate *Cheiroglossa* from *Ophioderma* was the absence of marginal free veinlets in the latter genus. In the fronds of *O. palmatum* studied, free marginal veinlets ranged from none to many, often in the same plant; obviously such a character is insufficient for generic circumscription.

Indument.—Neither the scales, which cover the rhizome apex, nor the trichomes found at the base of the petiole, show any structural peculiarities that make them useful taxonomically. Likewise, the wooly tomentum of some *Botrychium* species should not be used to segregate taxa. In addition to the material cited above, the following specimens were examined for their indument: Cerro de Zurquí, 2000 m, *Gómez 3505* (CR); Santa Cruz de Turrialba, 1500 m, *Poveda* (CR 59852); Around San Ramón, Pcia. Alajuela, *Brenes 179* (CR); Alto de Pacuare, *Gómez 3436* (CR).

Spores.—The spores seen through a light microscope are quite uniform. It is possible that the scanning electron microscope would reveal some variation in spore wall sculpturing that correlates with habitat or geographical distribution.

From the above, I feel certain that *O. palmatum* L. is quite variable and that the criteria used to segregate other taxa are not consistent. Nevertheless, there may be some constant, infraspecific taxa that have a distinct geographical range. But to discover these will require careful analyses of populations. At present I propose that subg. *Cheiroglossa* be considered monotypic, with the following synonymy:

Ophioglossum palmatum L. Sp. Pl. 2: 1062. 1753.

Cheiroglossa palmata (L.) Presl, Suppl. Tent. Pterid.: 57. 1845.
Ophioderma palmata (L.) Nakai, Bot. Mag. Tokyo **39:** 193. 1925.
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Cheiroglossa austrobrasiliensis Brade, Bradea **1:** 30, *t. 1*. 1970.

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Anatomical Studies of the Neotropical Cyatheaceae. I. Alsophila and Nephelea

TERRY W. LUCANSKY*

The taxonomic treatment of the Cyatheaceae has undergone numerous revisions as summarized in previous studies (Tryon, 1970; Gastony, 1973; Lucansky, 1974). Earlier research has shown the taxonomic importance of anatomy and morphology to the study of this group of ferns (Holttum & Sen, 1961; Sen, 1964; Lucansky, 1974; Lucansky & White, 1974). Yet, despite this renewal of interest in the tree ferns, comparative anatomical data are almost totally lacking for the neotropical species.

Tryon's (1970) revised classification of the Cyatheaceae recognizes three basic evolutionary lines among the squamate genera, based upon petiole scale characters. The genera *Alsophila* and *Nephelea*, with structurally marginate petiole scales having dark apical setae, constitute one evolutionary line. Similarities in the sporogenetic pattern, spore morphology, basal pinna structure, and potential for squaminate spine development also demonstrate a close phyletic relationship between these two genera (Gastony, 1973, p. 83).

An attempt is made to determine whether the proposed phyletic relationship between *Alsophila* and *Nephelea* is supported by anatomical data. Our knowledge of anatomical data for the New World tree ferns is also increased.

The following species were used in this study: *Alsophila salvinii* Hook., *A. engelii* Tryon, *Nephelea erinacea* (Karst.) Tryon var. *erinacea*, and *N. polystichoides* (Christ) Tryon. Voucher specimens are on file in the herbarium of Duke University. Developing shoot tips were collected in the moist, tropical, mountainous regions of Costa Rica and Venezuela. The plant materials were killed and fixed in formalin-acetic acid-alcohol (FAA) and sectioned on a "macrotome" (Lucansky, 1976b). The sections (slices) were partitioned into manageable sizes, dehydrated in a tertiary-butyl alcohol series, and embedded in paraffin (Johansen, 1940). Sections (8 μm) were made and stained with safranin-fast green. Parts of stained sections were photographed with a 35 mm Zeiss C35 camera, whereas entire sections (slices) were photographed with a 35 mm single-lens reflex camera.

RESULTS AND DISCUSSION

Based on habit, stem and petiole indument, stelar pattern, and nodal anatomy of mature specimens, *Alsophila* and *Nephelea* show striking similarities and a close phyletic relationship (Lucansky, 1974; Lucansky & White, 1974). Members of both genera are arborescent, with the upright habit being the derived condition in the Cyatheaceae (Bower, 1912, p. 293). Both genera are characterized by petiole scales that are differentiated into body and marginal cells and possess an apical seta. The cellular differentiation of the petiole margin in some species of *Alsophila* is similar to that of *Nephelea*. Certain species of both genera may bear setae on

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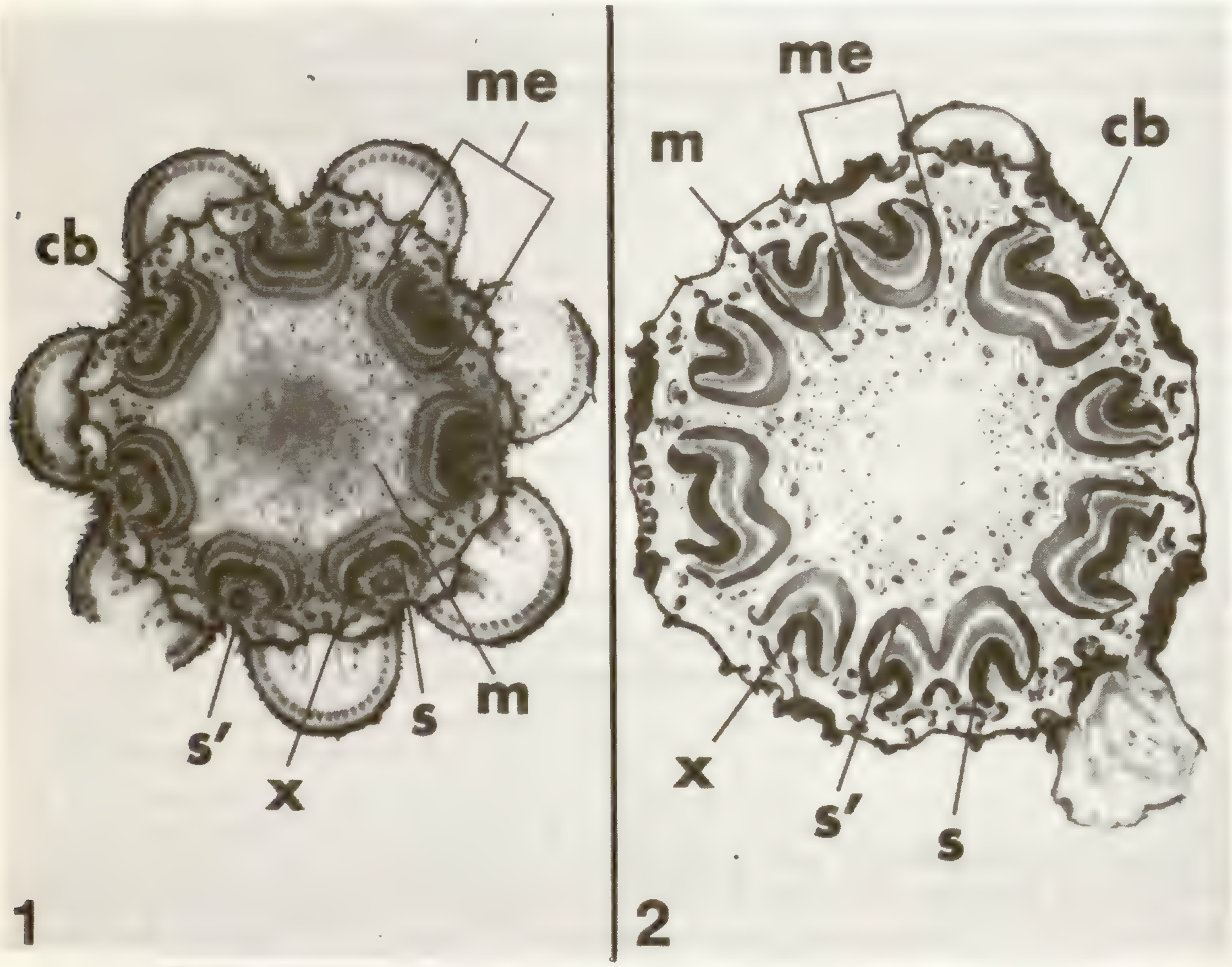
the margin or body of the scale (Tryon, 1970). *Alsophila* petioles typically lack spines, but if present they are corticinate, whereas *Nephelea* petioles have black, squaminate spines. Yet, squaminate spine development similar to that in *Nephelea* has been observed in *A. auriculata* (Tard.) Tryon (Tryon, 1970, p. 26).



Transections of tree-fern stems (dictyosteles). FIG. 1. *Nephelea erinacea* var. *erinacea*, × 0.7. FIG. 2. *Alsophila engelii*, × 1.2. cb = cortical bundle, m = medullary bundle, me = meristele, s = external stelar sheath, s′ = internal stelar sheath, x = xylem.

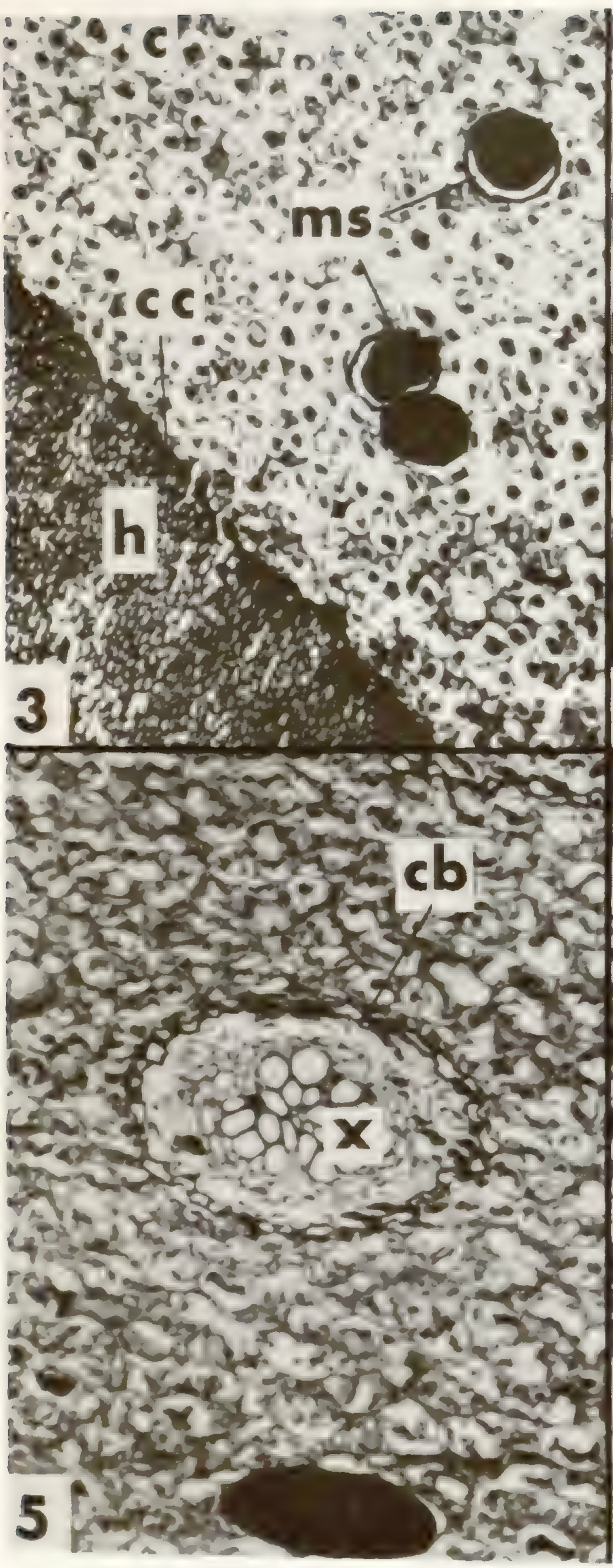
The stelar pattern in the mature stem is similar in all squamate genera, including *Alsophila* and *Nephelea* (Lucansky, 1974). In all species in this study the stelar pattern is a dictyostele composed of individual meristeles each surrounded by sclerenchymatous tissue (*Figs. 1* and *2*). The dictyostelic pattern is the result of the overlapping and lengthening of leaf gaps.

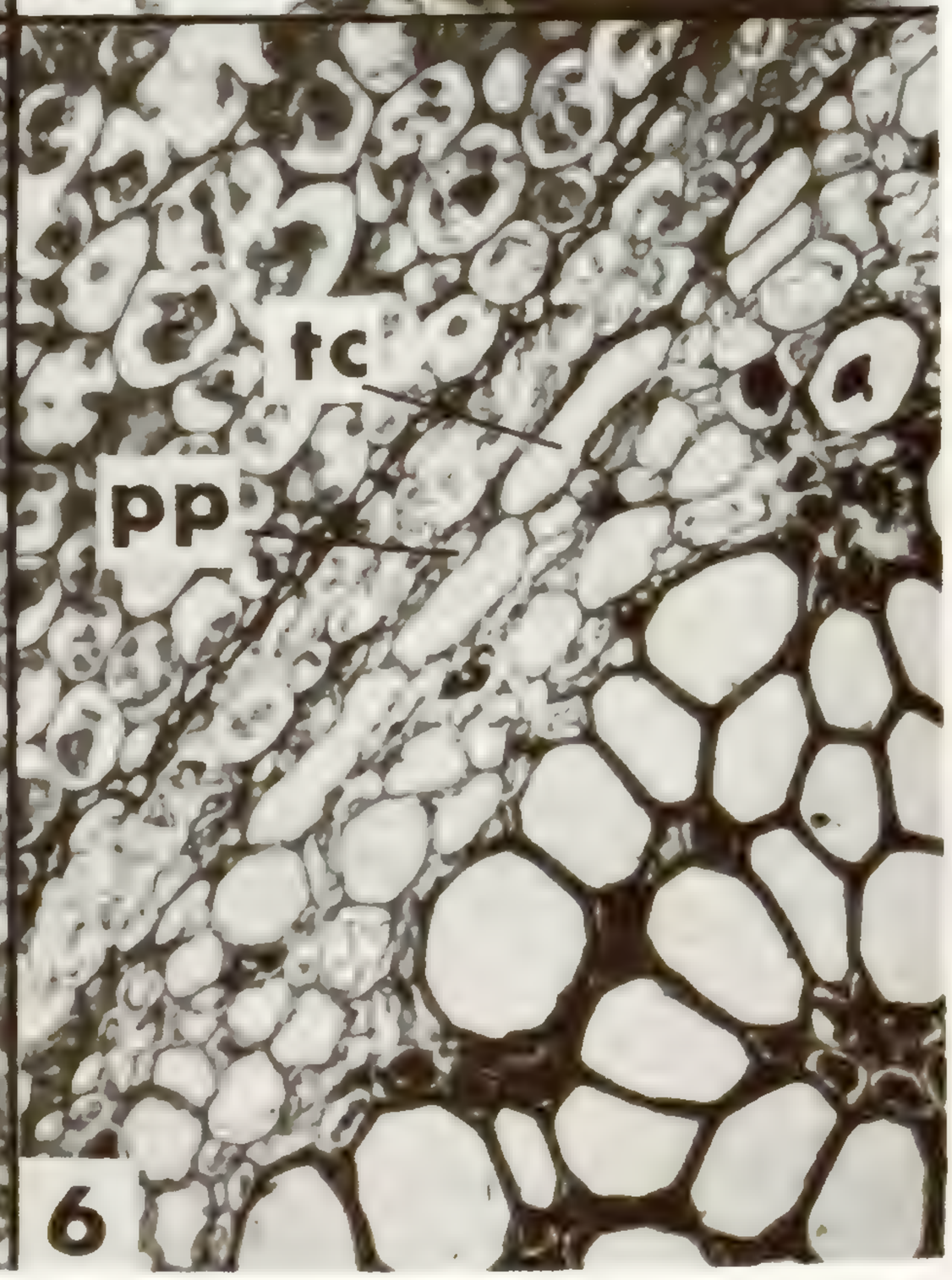
Stem transections of *Alsophila* and *Nephelea* reveal similar anatomical features. A single-layered epidermis composed of either elongate or irregularly-shaped cells is typically sloughed off in mature sporophytes. In *Culcita* and *Cystodium*, the outer walls of these cells may be thickened (Sen & Mittra, 1966) or cutinized (Sen, 1968). The outermost layer of the stem in *Alsophila* and *Nephelea* is a hypodermis composed of two zones of variable thickness, as previously reported (Ogura, 1927, pp. 174, 211; Ogura, 1938, p. 354; Sen, 1964). The outer zone is composed of thick-walled, irregularly-shaped parenchyma cells that typically are partially sloughed off. Sen (1968) reported that in *Culcita macrocarpa*

Presl these cells are formed by secondary sclerosis of the walls with the retention of the nucleus. The inner zone consists of sclerenchyma fibers (with lateral wall pitting) that are more isodiametric, smaller in diameter, and possess thinner walls than the parenchyma cells. Infrequently a middle zone composed of transitional parenchyma-sclerenchyma cells occurs in *N. polystichoides*, or the hypodermis is composed solely of sclerenchymatous fibers, as in *A. salvinii*. Ogura (1938, p. 354) also reported that the hypodermis may be composed entirely of sclerenchyma fibers. In all species in this study, the cortex is composed of large, irregularly shaped parenchyma cells with numerous starch grains, although Sen (1964) reported that a band of sclerenchyma tissue may occur between cortical layers of parenchyma in *Dicksonia* and *Culcita*. In the present study, mucilage-sac cells are randomly distributed in the cortex, either singly or in groups of 2 or 3 (*Fig. 3*), and form an articulated laticifer system. Schütze (1906) called these idioblasts excretion containers, rather than secretion cells, and reported that they contain fatty acids or tannin, whereas Ogura (1938, p. 356) found that they contained slime. Although no mucilage-sac cells are found in *Culcita* (Christensen, 1938) or *Cibotium barometz* (L.) J. Smith (Ogura, 1927, p. 277), such idioblasts have been reported for *Dicksonia squarrosa* (Forst.) Swartz (Williams, 1925). Previous workers have found cubical cells in the cortex of *Cyathea* and *Culcita* (Sen, 1964) and irregular patches of sclerenchyma tissue and intercellular spaces in the cortical zone of *Cystodium sorbifolium* J. Smith (Sen & Mittra, 1966).

A distinctive layer occurs between the hypodermis (sclerenchyma fibers) and the cortex (parenchyma cells). The cells that comprise this layer are greatly thickened on three walls (the wall proximal to cells of cortex remains thin-walled), and each cell contains a single, large irregular crystal (*Fig. 4*). These cells have been designated "cubical cells" by earlier workers (Ogura, 1927, p. 176, 1938, p. 354; Holttum & Sen, 1961; Sen, 1964). However, occasionally they do not possess a distinctive shape. Hence, the designation "cubical" is not warranted in all species. In transection the greatly thickened walls typically mask all features of this layer (*Fig. 3*), whereas in longitudinal section the isodiametric shape (if present) and large crystal are readily visible (*Fig. 4*). These cells are thick-walled parenchyma cells, based upon their living protoplast, wall morphology, position, and resemblance to parenchyma cells in younger stems. Sen (1964) felt that the cubical cells were not sclerenchyma cells, based upon their position, rate of cell division, and cellular inclusions, whereas Ogura (1938) reported that they were sclerenchyma cells. The crystalloid mass in each cubical cell is insoluble in H_2SO_4 (Holttum & Sen, 1961) and is thought to be composed of silica (Sen, 1968). In this study, the cubical cells form a continuous, distinctive layer, which infrequently is two cells thick in *N. polystichoides*. Numerous cubical cells are randomly distributed in the cortex of *Dicksonia squarrosa* and *Thyrsopteris* (Sen, 1964), whereas solitary cubical cells occur in *Lophosoria* (Holttum & Sen, 1961).

In *N. polystichoides*, *N. erinacea* var. *erinacea*, and *A. engelii*, vascular bundles occur in the cortical zone (Lucansky, 1974); such bundles are found only in certain members of the Cyatheaceae. These vascular bundles are surrounded by a distinct endodermis filled with tanniferous substances (*Fig. 5*). A pericycle of 1–3



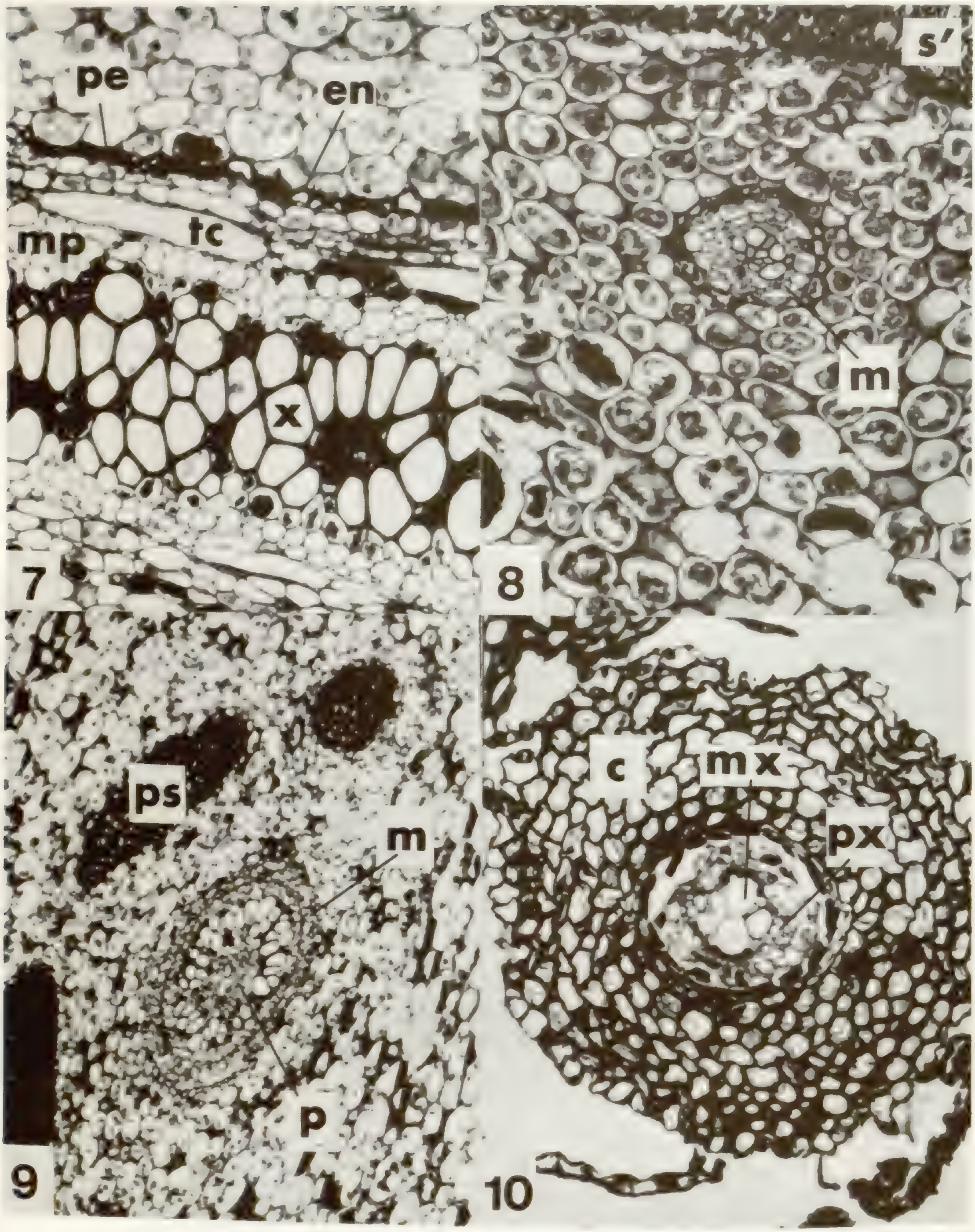


Anatomical details of tree-fern stems. FIG. 3. Mucilage-sac cells (laticifers) in cortical zone of *Nephelea polystichoides*, × 117. FIG. 4. Cubical cells with crystals in *Alsophila salvinii* forming boundary between hypodermis and cortex, × 31. FIG. 5. Small cortical bundle in *N. polystichoides*, × 128. FIG. 6. Tangential cells in meristele of *N. erinacea* var. *erinacea*, × 109. c = cortex, cb = cortical bundle, cc = cubical cells, cr = crystal, h = hypodermis, ms = mucilage-sac cell, pp = protophloem, tc = tangential cell, x = xylem.

layers of parenchyma cells encircles the primary phloem, which is composed of both sieve cells and phloem parenchyma. In all species studied, no tangential cells are found in the cortical bundles, regardless of their size. Depending upon the size of the cortical bundles, a parenchymatous pith may be found in the center of the primary xylem. Small bundles are protostelic (*Fig. 5*), whereas larger cortical bundles possess a parenchymatous pith. Ogura (1938, p. 362) reported that large bundles may have a cavity filled with tyloses. The primary xylem typically is composed of scalariform tracheids, with xylem parenchyma interspersed among these xylary elements in the larger bundles. Xylem maturation is mesarch. The smaller cortical bundles typically lack a sheath composed of sclerenchyma fibers, whereas the larger bundles may possess a partial sheath. In contrast, an earlier study indicated that those cortical bundles located along the external stelar sheath usually lack a sheath, and infrequently may be completely sheathed (Lucansky, 1974). The origin and fate of the cortical bundles is discussed in this earlier paper (Lucansky, 1974).

Transections of the stem show 3-10 meristeles, depending upon the species (*Figs. 1* and *2*). Each meristele is surrounded by an external and an internal stelar sheath composed of sclerenchyma fibers with conspicuous lateral wall pitting. The presence of sclerenchymatous tissue around the individual meristeles is a characteristic feature of the Cyatheaceae. The fibers of the stelar sheaths are typically longer and larger in diameter than those of the hypodermis. Both stelar sheaths are delimited externally and internally by a single layer of cubical cells, although the crystalloid mass is frequently lacking in these cells. Typically the external stelar sheath is more heavily lignified and thicker-walled than the internal stelar sheath, and appears darker in color (*Figs. 1* and *2*). The stelar sheaths, together with the hypodermis, provide support for the stem and the large leaves (Schütze, 1906). Both stelar sheaths arise from localized areas of sclerenchyma cells that undergo fusion to form a continuous sheath (Lucansky, 1976a). A parenchymatous zone that contains numerous mucilage-sac cells separates the stelar sheaths from the meristele and may function in the conduction and storage of carbohydrates (Schütze, 1906).

Each meristele is an amphicribral bundle and is delimited by a distinct endodermis filled with tanniferous substances. Distinct Casparian strips are lacking in the radial walls of these cells. A pericycle composed of 1-3 rows of parenchyma cells completely encircles the primary phloem. The latter tissue is composed of a single layer of protophloem (small, elongate cells), a distinctive layer of tangential cells, and several layers of metaphloem composed of sieve cells and phloem parenchyma (*Figs. 6* and *7*). Although Ogura (1927, p. 176, 1938, p. 361) reported that the protophloem was usually compressed, thick-walled, and swollen, no evidence of mechanical stress on these cells is found in this study (*Fig. 6*). Frequently the protophloem and metaphloem are indistinguishable in all species studied, or the former tissue may be lacking. Although earlier workers indicated that the primary phloem is composed of distinct layers (rows) of phloem parenchyma and sieve cells (Schütze, 1906, p. 353; Ogura, 1927, p. 177), these two cell types are randomly interspersed in the species in the present study. The sieve



Anatomical details of tree-fern stems. FIG. 7. Meristele of *A. salvinii* showing tangential cells, × 171. FIG. 8. Small medullary bundle near internal stelar sheath in *A. engelii*, × 110. FIG. 9. Large medullary bundle with partial sheath and pith in *N. erinacea* var. *erinacea*, × 105. FIG. 10. Transection of root of *N. erinacea* var. *erinacea*, × 104. c = cortex, en = endodermis, m = medullary bundle, mp = metaphloem, mx = metaxylem, p = pith, pe = pericycle, ps = partial sheath, px = protoxylem, s′ = internal stelar sheath, tc = tangential cell, x = xylem.

cells possess scalariform sieve plates and sieve areas on their lateral walls. Sen (1964) found mucilage-sac cells in the primary phloem, whereas in the present study these cells are simply phloem parenchyma filled with mucilage.

The tangential cells are large and elongate tangentially in transection (*Fig. 6*), and form a characteristic feature of the Cyatheaceae. These cells typically occur between the protophloem and metaphloem, but may represent the outermost layer of the primary phloem, if the former layer is lacking. They represent specialized sieve cells that are devoid of nuclei, possess sieve areas on their lateral walls, and accumulate callose (Sen, 1964), although they have been variously referred to as "false sieve tubes" (Schütze, 1906, p. 355) or mucilage cells (Ogura, 1927, p. 341). According to Ogura (1927, p. 342), these distinctive cells may be partially or entirely replaced in a given species by mucilage cells or longitudinally elongate cells (i.e., tangential cells are mucilage cells with a different orientation).

The primary xylem typically is composed of tracheids with scalariform end plates. The xylem parenchyma contains mucilage droplets interspersed among the tracheids. Each meristele is composed predominantly of metaxylem, with the protoxylem poles difficult to discern (*Fig. 7*). Earlier studies have reported that protoxylem is usually absent in the primary xylem of mature stems (Ogura, 1927; Sen, 1964), although spiral tracheids are noted infrequently in the present study. Xylem maturation is mesarch in all species studied.

The pith is composed of large, irregularly-shaped parenchyma cells that contain numerous starch grains. Mucilage-sac cells are randomly distributed in the pith, either singly or in groups of 2 or 3. A distinctive cubical layer occurs between the internal stelar sheath and the pith, although crystals typically are lacking in these cells.

In all species studied, medullary bundles are scattered randomly in the pith (*Figs. 1* and *2*), and represent a characteristic feature of the Cyatheaceae. The number of these bundles varies according to the size of the pith (Lucansky, 1974). These accessory bundles are identical in cellular composition to the cortical bundles (*Figs. 5* and *8*). Ogura (1927, 1938, p. 362) reported that the larger bundles may contain a central cavity with tyloses, although none are noted in the present study. In the species studied, small medullary bundles are protostelic, whereas larger bundles possess a parenchymatous pith (*Figs. 8* and *9*). Occasionally a very large bundle may possess several parenchymatous areas within the primary xylem. Tangential cells typically are lacking in medullary bundles, although the largest bundles may possess these distinctive cells. Ogura (1927) also reported the absence of tangential cells in the medullary bundles of certain species, whereas Schütze (1906, p. 365) found that these cells were the major component of the primary phloem of these bundles in *A. manniana* (Hooker) Tryon (as *Cyathea usambarensis* Hieron.). The primary xylem is composed primarily of scalariform tracheids, with no protoxylem visible. Xylem maturation is mesarch in these bundles (Lucansky, 1976a). A partial sheath composed of sclerenchyma fibers may or may not be found associated with each medullary bundle (*Fig. 9*). Normally only the vascular bundles located along the internal stelar sheath lack a sheath (*Fig. 8*), although Ogura (1938) reported that medullary bundles usually

lack such tissue. Larger bundles in the pith typically possess a more extensive partial sheath than that associated with cortical bundles. A thorough discussion of the origin and fate of medullary bundles is given in previous papers (Lucansky, 1974; Lucansky & White, 1974; Lucansky, 1976).

Transections of the adventitious roots show similar anatomical features in all species (*Fig. 10*). Typically the epidermis is sloughed off in mature roots, and the outer cortex, which is composed of thick-walled parenchyma cells, forms the outer boundary of the organ. These cortical cells are irregularly-shaped and partially sloughed off, and the inner cortex is composed of isodiametric sclerenchyma fibers and typically forms the bulk of the cortical zone. Ogura (1927, p. 340) indicated a similar arrangement for the cell layers that comprise the cortex, whereas other workers found the position of these cell layers reversed in the cortical zone (Schütze, 1906; Sen, 1968). The endodermis is a single layer composed of cells filled with tanniferous substances, but lacks distinct Casparian thickenings on the radial walls. A pericycle 1-3 cells thick and composed of large, irregularly-shaped parenchyma cells surrounds the vascular tissue. The primary phloem consists of sieve cells and phloem parenchyma. The xylem is typically diarch with exarch maturation (*Fig. 10*), although triarch and tetrarch xylem occasionally occur in larger roots. Longitudinal sections reveal primarily scalariform-pitted metaxylem, with some spiral and transitional (reticulate-scalariform) protoxylem.

Root traces originate either from the meristele or from the base of leaf traces and pass obliquely through the cortex. Ogura (1927) reported that the amount of xylem parenchyma increases and the number of tracheids diminishes during this passage.

Leaf traces arise at successive levels in the leaf gap and proceed to the petiole, where they form a much-dissected vascular pattern that is basically similar for all four species studied (Lucansky & White, 1974). The leaf traces vary in shape and are spherical-ellipsoidal to horseshoe-shaped, depending upon proximity to the petiole base. They are identical in cellular composition to the accessory bundles. The xylary elements are primarily metaxylem, with protoxylem located at the concavity of the vascular tissue in the horseshoe-shaped configuration.

The individual petiole strands are horseshoe-shaped and vary in number, depending upon the genus (Lucansky & White, 1974). The single-layered epidermis is sloughed off in mature plants, and a thick-walled parenchymatous zone represents the peripheral layer of the petiole. The ground tissue, composed of thin-walled parenchyma cells containing numerous mucilage droplets, comprises the bulk of the petiole. Cellular composition of the stele of each petiole strand (U- or V-shaped) is similar to that of a leaf trace, with protoxylem restricted to a median position on the concave side of the vascular tissue. Although previous workers reported that the protoxylem may partially disintegrate and form a cavity with tyloses (Schütze, 1906; Ogura, 1927, p. 343), none are found in the present study.

Based upon comparative anatomical data, *Alsophila* and *Nephelea* show striking similarities and represent closely-related genera. These data also support recent phyletic conclusions for these taxa (Tryon, 1970; Gastony, 1973, 1974).

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Prothallus Morphology in some Tectarioid Ferns

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Among the tectarioid ferns, studies of the prothalli have been made in *Arcypteris* and *Pleocnemia* (Atkinson, 1970), *Quercifilix* (Nayar, 1960), and *Tectaria* (Kachroo, 1956; Mahabale & Venkateswaran, 1959; Stokey, 1960; Nayar & Kaur, 1964; Srivastava, 1968). In other tectarioid fern genera no such studies have been made, although Stokey (1960, pp. 82-84) reported the hair types occurring in some genera, including *Ctenitis, Heterogonium,* and *Pteridrys*. The present study concerns ten species of tectarioid ferns: *Ctenitis ampla* (Humb. & Bonpl. ex Willd.) Ching,[2] *C. currori* (Mett. ex Kuhn) Tardieu, *C. eriocaulis* (Fée) Alston, *C. recedens* (J. Smith ex Moore) Copel., *Pteridrys australis* Ching ex C. Chr. & Ching, *Tectaria devexa* (Kunze) Copel., *T. fuscipes* (Wall. ex Bedd.) C. Chr., *T. heracleifolia* (Willd.) Underw., *T. leuzeana* (Gaud.) Copel., and *T. variolosa* (Wall. ex Hook.) C. Chr.

Spores of all the species except *T. fuscipes* and *T. leuzeana* were obtained by Prof. B. K. Nayar, of Calicut University, during his visit to England in 1972 from plants grown at the Royal Botanic Gardens, Kew. Spores of *T. devexa, T. fuscipes,* and *T. variolosa* were taken from plants grown at the National Botanic Gardens, Lucknow. Observations were made on prothalli raised on sterilized Knop's agar medium maintained at 23-25°C under 600 ft-c light intensity for 8 hours daily.

OBSERVATIONS

Prothallus development.—In all the species studied, spore germination (*Figs. 1* and *2*) is of the *Vittaria* type (Nayar & Kaur, 1968), and prothallus development is of the *Aspidium* type (Nayar & Kaur, 1969, 1971). All variations of the Aspidium type of prothallial development were found in all the species studied. The germ filament is usually 2-5 cells long (*Figs. 3* and *4*), as reported in species of *Tectaria* (Nayar & Kaur, 1964), *Quercifilix* (Nayar, 1960), and *Arcypteris* and *Pleocnemia* (Atkinson, 1970). However, the germ filaments may be more than five cells long in *C. eriocaulis* and *T. heracleifólia,* and are up to ten cells in the former species (*Fig. 5*) before any longitudinal divisions occur. Some of the filaments and young prothalli of *C. eriocaulis* and *T. devexa (Figs. 21-23)* produce lateral branches with each branch resembling an individual prothallus, as also has been reported in *T. variolosa* (Nayar & Kaur, 1964).

Plate formation may be initiated by a longitudinal or oblique wall in the terminal cell *(Figs. 7-9),* as also is known in *Tectaria* (Nayar & Kaur, 1964) and in *Arcypteris* and *Pleocnemia* (Atkinson, 1970), or it may be in the penultimate cell *(Figs. 10* and *11),* as in *Quercifilix* (Nayar, 1960) and commonly in *T. variolosa*. Both conditions also have been observed in the prothalli of the same species (e.g., *C. currori, C. eriocaulis, T. devexa, T. fuscipes,* and *T. heracleifolia).*

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[1]The authors are thankful to Dr. T. N. Khoshoo, Deputy Director-in-Charge, National Botanic Gardens, for providing facilities and giving encouragement during the course of this study.

[2]Very likely this plant is the commonly cultivated *C. sloanei* (Poepp.) Morton (see Morton, 1969).

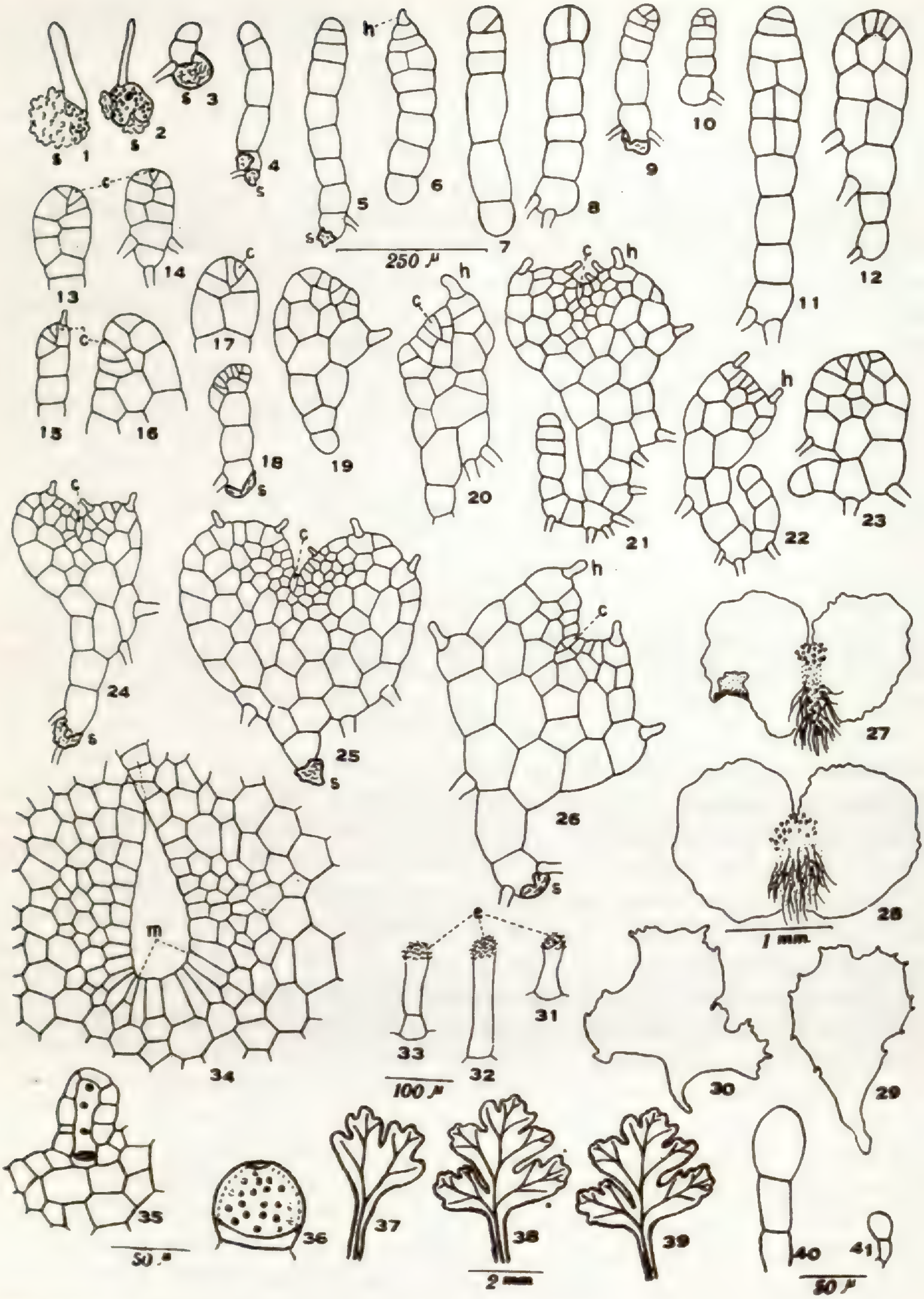
When the meristematic cell forms from the terminal cell, it may be formed by a single wall oblique to the longitudinal wall of the terminal cell *(Figs. 13* and *14)* in *C. currori, T. devexa, T. fuscipes,* or sometimes in *T. heracleifolia* by two walls, the first oblique to the longitudinal wall of the terminal cell and the second oblique to the first *(Fig. 17)*. The other daughter cell of the terminal cell may form a hair (*Fig. 15*); usually hair formation is quite delayed.

In those prothalli where the penultimate cell divides to form the meristic cell, first one of the daughter cells divides further and then the meristematic cell is initiated. In such prothalli the terminal cell may terminate in a hair, as it rarely does in *T. devexa (Fig. 6),* and as described in *Quercifilix* (Nayar, 1960); again, hair formation often is quite delayed *(Figs. 10* and *11)*.

Prothalli are somewhat one-sided, with the meristematic cell not exactly apical in prothalli where the first divisions start in the penultimate cell. This is quite often seen in *T. fuscipes (Fig. 16)* and in *T. heracleifolia (Fig. 18)*. In such cases, the cells below the meristematic cell divide actively so that the meristematic cell soon becomes apical. The obconical meristematic cell actively cuts off daughter cells on either side and the prothallus becomes spatulate with more or less flat apical region in *T. devexa (Fig. 20)* and *T. variolosa (Fig. 19)*. Later the prothallus apex becomes notched, with the meristematic cell at the bottom of the notch *(Figs. 21, 24* and *25)*. In species like *C. eriocaulis, T. devexa, T. fuscipes, T. leuzeana,* and *T. variolosa,* ameristic prothalli are also present (*Figs. 12* and *22)*. The meristematic cell soon is replaced by a multicellular meristem in the usual way (*Fig. 26*), as described by Nayar and Kaur (1964). By this time marginal hairs are fully developed and superficial hairs have started to develop.

Mature prothallus.—In all the tectarioid ferns studied, the mature prothallus is cordate and much broader than long *(Figs. 27* and *28)*. The wings overlap each other in the region anterior to the apical notch in most of the species, but do not in *Pteridrys australis*. The apical meristem is normally broad and composed of 6-8 slender, elongate cells *(Fig. 34)*. The midrib is narrow and spindle-shaped in most of the species studied *(Fig. 27),* although it may be very broad in *P. australis (Fig. 28)*. The mature prothallus may be elongate, especially in *C. currori (Fig. 29)* and in *T. fuscipes,* or it may bear irregular, ameristic lobes in *T. leuzeana (Fig. 30)*. Mature prothalli bear hairs profusely on the margin and surface. These hairs are mostly unicellular, sparsely chlorophyllous, and usually are crowned by an extra-cellular, cap-like secretion, and so resemble the hairs reported in most of the aspidiaceous ferns. These hairs may be short and club-shaped *(Fig. 31)* or elongate and papillate *(Fig. 32)*. Two-celled, long hairs *(Fig. 33)* have been observed very rarely. Such hairs are reported to occur in *Pleocnemia conjugata* (Stokey, 1960, p. 83). However, branched, multicellular hairs like those reported in species of *Tectaria* and *Pteridrys* (Stokey, 1960; Nayar & Kaur, 1964; Atkinson, 1973) and long, slender, glandular hairs associated with acicular hairs as reported in *Ctenitis (Lastreopsis) effusa* (Atkinson, 1970, p. 82) have not been observed in the present study.

Sex organs.—In the tectarioid ferns studied, sex organs are similar to those reported earlier in species of *Tectaria.* Antheridia are produced on the lower



Stages in the development of prothalli and juvenile leaves of *Ctenitis*, *Pteridrys*, and *Tectaria*. FIG. 1. Vittaria-type germination in spores of *C. recedens*. FIG. 2. Same, *C. eriocaulis*. FIG. 3. Germ filaments of *C. recedens*. FIGS. 4, 5. Same, *C. eriocaulis*. FIG. 6. Germ filament of *T. devexa*

surface of the prothalli soon after the apex of the prothallus becomes cordate and are restricted to the midrib region. Under crowded conditions, antheridia are also produced by germ filaments even before the cell plate is formed, and so are marginal. Archegonia are formed later than antheridia and are superficial on the lower surface in the region of the midrib near the apical notch. Antheridia are globose *(Fig. 36)* with the basal cell usually saucer-shaped. Archegonia possess short, slightly curved necks which generally are 3-5 cells long *(Fig. 35)*.

Juvenile leaves.—Among the species studied, only *C. ampla* and *C. recedens* produced juvenile sporophytes. Fertilization takes place 5-6 months after the spores are sowed, and young sporophytes are soon formed. The first juvenile leaf is obcuneate with a single, dichotomously divided vein, as shown in species of *Tectaria* (Nayar & Kaur, 1964) and *Pleocnemia* (Atkinson, 1970). Soon the lamina becomes lobed, and the single-forked vein divides dichotomously so that each ultimate vein supplies a single lobe (*Fig. 37*). The lamina margin becomes considerably lobed, and the midrib forms (*Fib. 38*), usually by the fourth or fifth leaf, as also has been described in *Tectaria* (Nayar & Kaur, 1964) and *Pleocnemia* (Atkinson, 1970). By approximately the eighth leaf, the lamina becomes pinnate with simple venation (*Fig. 39*), as described in *T. fuscipes*. Unicellular and multicellular uniseriate hairs similar to those present on the prothalli cover the stipes and laminae of the juvenile leaves. In addition, some very small, two-celled, club-shaped (*Fig. 41*) and three-celled, elongate (*Fig. 40*) hairs also occur on the juvenile leaves.

CONCLUSIONS

The present study has shown that the types of spore germination and prothallial development are similar in all the tectarioid fern genera studied. Branched hairs reported earlier in *Tectaria* (Nayar & Kaur, 1964), *Pteridrys* and *Heterogonium* (Stokey, 1960, pp. 83, 84; Atkinson, 1970, p. 82), and *Quercifilix* (Nayar, 1960) are absent in the species of the present study, as they are in *Pleocnemia* and *Arcy-*

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showing terminal hair. FIGS. 7, 8. Germ filaments showing initiation of plate formation in the terminal cell in *T. fuscipes*. FIG. 9. Same, *T. heracleifolia*. FIG. 10. Germ filament showing initiation of plate formation in the penultimate cell of *T. heracleifolia*. FIG. 11. Same, *T. devexa*. FIG. 12. Ameristic thallus of *T. fuscipes*. FIGS. 13, 17. Young prothalli showing formation of the meristematic cell of *T. devexa*. FIG. 14. Same, *C. currori*. FIG. 15. Same, *C. eriocaulis*. FIG. 16. Same, *T. fuscipes*. FIG. 18. Same, *T. heracleifolia*. FIG. 19. Spatulate prothalli showing flat apical region in *T. variolosa*. FIG. 20. Same, *T. devexa*. FIGS. 21, 22. Branched prothalli of *C. eriocaulis*. FIG. 23. Same, *T. devexa*. FIG. 24. Young prothalli showing meristematic cell at the bottom of the apical notch in *P. australis*. FIG. 25. Same, *C. currori*. FIG. 26. Young prothallus of *T. variolosa* showing initiation of replacement of meristematic cell by multicellular meristem. FIG. 27. Mature prothallus of *C. eriocaulis*. FIG. 28. Same, *P. australis*. FIG. 29. Same, *C. currori*. FIG. 30. Same, *T. leuzeana*. FIGS. 31-33. Marginal hairs on the prothalli of *C. recedens*. FIG. 34. Portion of a mature prothallus of *C. ampla* showing multicellular meristem. FIG. 35. Vertical section through the archegonium of *C. ampla*. FIG. 36. Mature antheridium of *P. australis*. FIGS. 37-39. Stages in the development of juvenile leaves of *C. ampla*. FIGS. 40, 41. Hairs on the juvenile leaves of *C. recedens*. The abbreviations are: c = meristematic cell, e = extracellular cap, h = hair, m = multicellular meristem, and s = spore.

pteris (Atkinson, 1970). However, prothalli of five species of *Tectaria* in Stokey's cultures did show the presence of multicellular or branched hairs or both (Stokey, 1960). Thus Stokey's observations and the present ones are in agreement that the occurrence of branched hairs on tectarioid prothalli does not happen regularly.

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The Occurrence of Thelypterin in Ferns

G. H. DAVIDONIS*

Two inhibitory substances, thelypterin A and B, have been isolated from the fern *Thelypteris normalis* (C. Chr.) Moxley. High concentrations of the thelypterins inhibit cell division in *T. normalis* gametophytes, whereas at lower concentrations the gametophytes are ameristematic (Davidonis & Ruddat, 1974). Sporophyte roots and pre-elevation stage leaves (those just prior to petiole elongation and leaf uncurling) contain thelypterins A and B (Davidonis & Ruddat, 1974); the structure of neither compound is known. This paper reports the occurrence of thelypterins in the culture medium of *T. normalis* gametophytes. Also, other fern genera were examined for thelypterins.

MATERIALS AND METHODS

Spores of *T. normalis* were collected from sporophytes grown in the Wheaton College greenhouses. Spores were surface sterilized with 0.5% sodium hypochlorite and sown in flasks containing modified Knudson's medium (Steeves et al., 1955) supplemented with trace elements (Nitsch, 1951) and placed on a rotary shaker under continuous illumination at 25°C.

Expanding fern leaves were completely immersed for 90 hours in a liter of distilled water under continuous illumination at 25°C. Fern roots were prepared as previously described (Davidonis & Ruddat, 1973). Culture medium in which gametophytes had grown (conditioned culture medium) and distilled water containing leaf or root diffusion products (diffusates) were concentrated under reduced pressure in a rotary evaporator, acidified to pH 4.0, and extracted with ethyl acetate. The ethyl acetate fraction was dried, evaporated, and chromatographed on thin-layers of Silica-gel pF 254 (Merck) in ethyl acetate-isopropanol (7:3, V/V). The chromatogram was divided into six zones which were removed and eluted with methanol. One, or occasionally two, bands on the chromatogram fell into each zone. The solvent was evaporated and the fraction dissolved in distilled water and assayed by the *T. normalis* spore bioassay (Davidonis & Ruddat, 1973). The criteria for thelypterins were: a positive Ehrlich reaction for thelypterin A (pink) and no reaction for thelypterin B, co-chromatography with thelypterins, and growth inhibition in the *T. normalis* spore bioassay.

RESULTS AND DISCUSSION

One liter of culture medium in which *T. normalis* gametophytes had grown for 35 days contained thelypterin A in an amount equivalent to that found in 2.5 g of fern root dry weight (Davidonis & Ruddat, 1973). Thelypterin B was not detected. A gametophyte producing large quantities of thelypterin A can inhibit the growth of other gametophytes, thereby reducing competition.

Thelypteris normalis leaf diffusates also contain thelypterin A but not thelypterin B. Excised croziers placed on agar release both thelypterin A and B into the medium (Davidonis & Ruddat, 1974). Therefore, foliar leaching may be an important means of releasing thelypterin A into the environment.

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Nine fern species belonging to seven genera were tested for thelypterins (*Table 1*). Root diffusates were used, except for *T. noveboracensis* (L.) Nieuwl. and *Phlebodium aureum* (L.) J. Smith, where leaf diffusates were tested because these two species had small root systems. Thelypterin A was released from *T. dentata* (Forsk.) E. St. John and *T. noveboracensis*, thelypterin B from the roots of *T. dentata*, *Pteris vittata* L., and *P. multifida* Poir. *Osmunda cinnamomea* L. leaves (but not roots) contained an inhibitor different from the thelypterins. The inhibitor co-chromatographed with thelypterin A but did not give a positive Ehrlich reaction. *Cyrtomium falcatum* (L.) Presl, *Dryopteris spinulosa* (O. F. Muell.) Watt, and *Pellaea viridis* (Forsk.) Prantl contained neither the thelypterins nor other inhibitors.

TABLE 1. THELYPTERINS IN FERNS.

Species	*Source of Material*	*Thelypterin* A	B	*Other Inhibitors*
	OSMUNDACEAE			
Osmunda cinnamomea	roots	–	–	–
O. cinnamomea	leaves	–	–	+
	PTERIDACEAE			
Pellaea viridis	roots	–	–	–
Pteris multifida	roots	–	+	–
P. vittata	roots	–	+	–
	THELYPTERIDACEAE			
Thelypteris normalis	roots	+	+	–
T. dentata	roots	+	+	–
T. noveboracensis	leaves	+	–	–
	DRYOPTERIDACEAE			
Cyrtomium falcatum	roots	–	–	–
Dryopteris spinulosa	roots	–	–	–
	POLYPODIACEAE			
Phlebodium aureum	leaves	–	–	–

The presence of inhibitors that can be leached from leaves or released from roots may prevent the establishment of gametophytes in the immediate vicinity of the sporophyte. This phenomenon may account for the general absence of gametophytes near sporophytes under natural conditions.

The results in *Table 1* suggest that thelypterin A could act as a chemotaxonomic marker of phylogenetic significance within the Thelypteridaceae. A recent classification (Nayar, 1970) suggests that the Thelypteridaceae and the Pteridaceae are not closely related.

This study was supported by a grant from Wheaton College, Norton, MA.

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Cystopteris fragilis in the Western Himalayas

S. S. BIR and CHANDER K. TRIKHA*

While working out the taxonomy of the genus *Cystopteris* Bernh. in India, Bir and Trikha (1973) segregated *C. fragilis* (L.) Bernh. into two forms in addition to f. *fragilis*. In the present paper the new forms are described and typified in conformity with the "International Code of Botanical Nomenclature." These forms can be distinguished using the following key:

KEY TO CYSTOPTERIS FRAGILIS IN THE WESTERN HIMALAYAS

1. Spores granulose .....2. *C. fragilis* f. *granulosa*
1. Spores echinate.
   2. Pinnules oblong, rhomboidal, obtuse at the apex, the lobes blunt and shallowly toothed. 1. *C. fragilis* f. *fragilis*
   2. Pinnules narrowly oblong, acute at the apex, the lobes acutely toothed. 3. *C. fragilis* f. *himalayensis*

1. Cystopteris fragilis f. fragilis. **Figs. 1A, B.**

ILLUSTRATIONS: Blasdell (1963, p. 81, pl. 2A-G), Bir and Trikha (1973, pp. 12-13, figs. 1-5).

SPECIMENS EXAMINED:

CANADA: Quebec: Corniche de grès, entre Bradore et Blanc Sablon, 6 Sept 1957, *A. Hende, H. Generux & P. Deslauriers* (PAN 3035). **INDIA: Himachal Pradesh:** Rohtang Pass, Kulu valley, western Himalayas, 3900 m, July 1966, *S. P. Khullar* (PAN 5393).

2. Cystopteris fragilis f. granulosa Bir & Trikha, f. nov. **Figs. 2A, B.**

A *Cystopteride fragili* f. *fragili* sporis granuloso-verrucosis differt.

Stipes stramineous to light brown, glossy, usually equal to or longer than the laminae; fronds 15-30 cm long, 4-8 cm wide; laminae linear-lanceolate to broadly ovate-lanceolate, resembling *C. fragilis* f. *fragilis* in frond outline, the pinnules broad with an obtuse apex; spores granular and warty.

ILLUSTRATIONS: Bir and Trikha (1973, pp. 13-15, figs. 6-7).

TYPE: Near Rahala, along the route to Rohtang Pass, Kulu Valley, Western Himalayas, Himachal Pradesh, India, 2700 m, 8 Oct 1964, *S. S. Bir* (PAN 5241).

PARATYPES:

INDIA: Himachal Pradesh: Rohtang Pass, Kulu Valley, western Himalayas, 5400 m, 8 Oct 1964, *S. S. Bir* (PAN 5242). **Kashmir:** Chandanwari, 2700 m, July 1959, *T. N. Khoshoo* (PAN 2406, 2407). **Tibet:** Dirankphu, Dolma la, along the route to Mount Kailash, 3000 m, 21 July 1956, *R. S. Pathania* (PAN 2408, 2409).

The chief feature of this form which distinguishes it from f. *fragilis* is the spores, which are echinate in f. *fragilis* and granulose-warty in f. *granulosa*. The spores, which Bir and Trikha (1973) considered rugose-verrucose, are redefined here as granulose in the light of SEM studies of Jermy and Harper (1971) on the spores of the *C. fragilis* complex in Europe.

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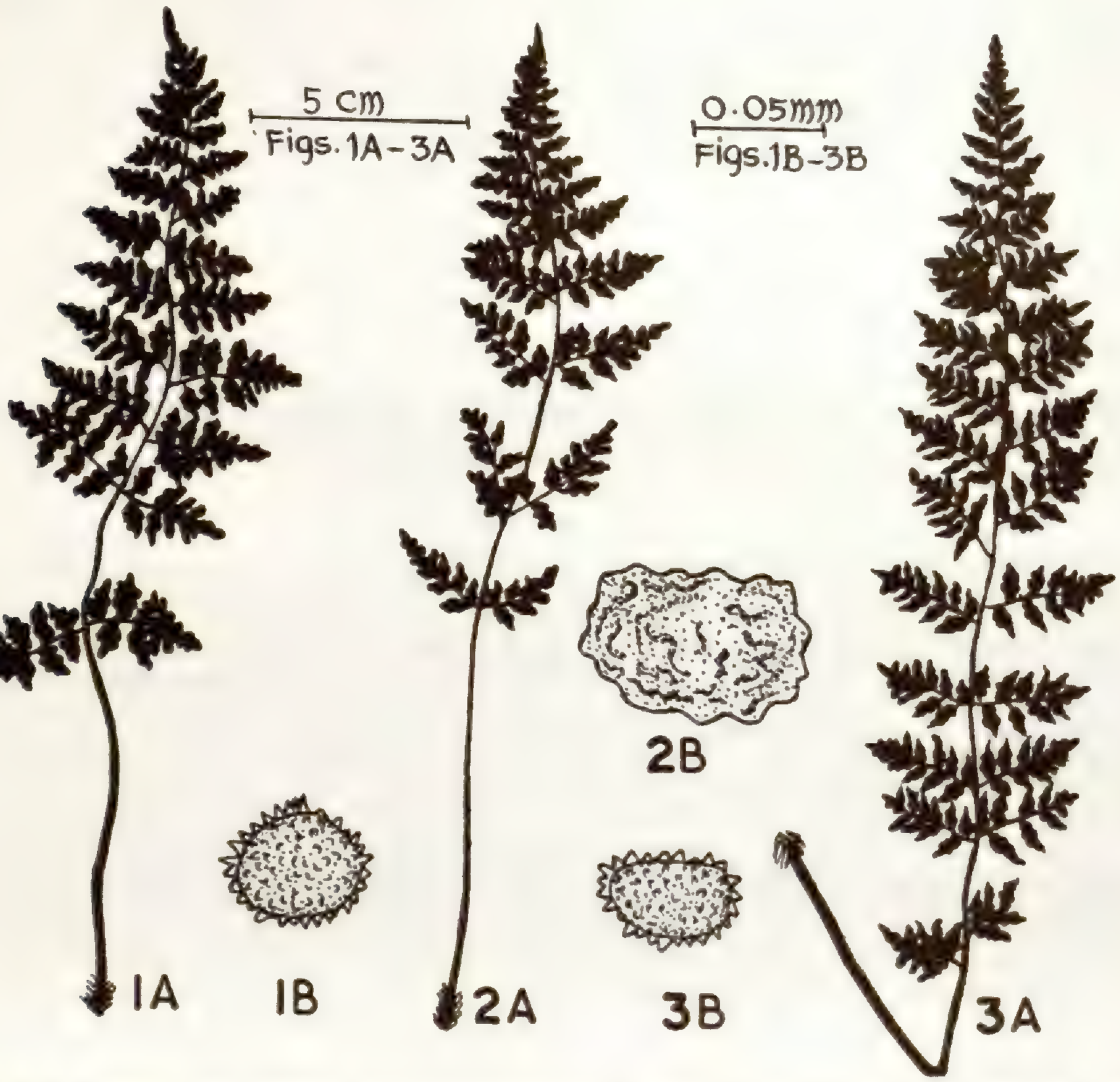
3. Cystopteris fragilis f. himalayensis Bir & Trikha, f. nov. Figs. 3A, B.

A *Cystopteride fragili* f. *fragili* pinnulis anguste oblongis apice acutis lobis dentatis dentibus acutis differt.

Pinnae broadly lanceolate, the pinnules narrow, oblong with an acute tip, cut ca. ¼ to ½ the way down to the costae into lobes with acute teeth; spores echinate.

ILLUSTRATIONS: Bir and Trikha (1973, pp. 14-15, figs. 8-9).

TYPE: Gulmarg, western Himalayas, Kashmir, India, 2700 m, July 1966, *S. P. Khullar* (PAN 5389).



FIGS. 1-3. Fronds and spores of *Cystopteris fragilis*. FIG. 1. Forma *fragilis*. FIG. 2. Forma *granulosa*. FIG. 3. Forma *himalayensis*.

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SHORTER NOTES

TWO NEW SITES FOR CERATOPTERIS THALICTROIDES IN TEXAS.—The Water Fern was first reported for Texas by Morton (Amer. Fern J. **57:** 13-14. 1967) from the spring-fed backwater of the San Marcos River at San Marcos in Hays County. Hannen (Amer. Fern J. **59:** 122. 1969) reported that this species was introduced into Spring Lake, the headwaters of the San Marcos River. Although the spring-fed area above Spring Lake Dam has been highly commercialized (it is now known as Aquarena Springs), *Ceratopteris thalictroides* (L.) Brongn. is quite abundant is shaded areas along the shoreline of Spring Lake. We also collected it in the river at San Marcos on 9 Aug 1975 *(Petrik-Ott 1002,* TAES, US). It grows most abundantly along the shaded banks of the San Marcos River to where the Blanco River joins it, about 5 km southeast of the springs.

We often frequent springs in search of fresh-water red algae, and so after seeing *C. thalictroides* in such abundance at San Marcos, we decided to look for it at other springs. We were rewarded by a new find on 10 Aug 1975 in the Comal River at New Braunfels, Comal County, where it was growing abundantly along the muddy banks below Comal Springs in Landa Park *(Petrik-Ott 1003,* TAES, US). On 7 Sept 1975 we found another station at Salado, Bell County, in a small spring which flows into Salado Creek about ¼ mile downstream from the State Highway 35 bridge across Salado Creek *(Petrik-Ott 1004,* TAES, US). However, we did not find it along the creek itself.

The two new sites for *C. thalictroides* extend its range in Texas 17 miles to the southwest and 75 miles to the north-northeast of the San Marcos locality. The three spring areas in Texas where this species is now known occur along the Balcones Fault, which runs south from Cedar Springs, north of Dallas, to the area of Carrizo Springs southwest of San Antonio. There are numerous springs along this fault line, and because the waters of at least the larger springs provide constant environmental conditions (of temperature, among others), we believe that *Ceratopteris* may persist for an indefinite time and that additional sites may be found.—*Aleta Jo Petrik-Ott, Department of Plant Sciences, College of Agriculture,* and *Franklyn D. Ott, Botany Section, Department of Biology, Texas A&M University, College Station, TX 77843.*

ADIANTUM CAPILLUS-VENERIS IN THE BAHAMA ISLANDS.—The discovery of *Adiantum capillus-veneris* L. in the Bahama Islands brings to 43 the number of pteridophytes now known to occur in that archipelago and in the Caicos and Turks Islands. Its collection data are: New Providence, on moist, east-facing walls of Fort Charlotte, Nassau, rather common in crevices between stone blocks, fronds drooping, March 26, 1976, *D. S. Correll & John Popenoe 46946* (FTG, NY, F, MO, US). Dr. John T. Mickel has kindly informed me that the specimen in the New York Botanical Garden herbarium reported as this species by W. C. Coker (no. 130) in Shattuck's "The Bahama Islands" (p. 248, 1905) is in reality *A. tenerum* Swartz.—*Donovan S. Correll, Fairchild Tropical Garden, Miami, FL 33156.*

VASCULAR CRYPTOGAMS AT A SITE DEGLACIATED IN 1880.—In the summer of 1974, I had the opportunity to observe the plant assemblages growing on recently deglaciated terrain of various ages at Glacier Bay National Monument in southeastern Alaska. According to Hultén (Flora of Alaska and Neighboring Territories. 1968. pp. 25-58), the ranges of 43 vascular cryptogams include the Glacier Bay area. Twenty-four of these have been recorded from the outer coast of Glacier Bay National Monument (Streveler, G. P., I. A. Worley, C. J. Terry, & R. J. Gordon. 1973. Dixon Harbor Biological Survey, National Park Service, Glacier Bay National Monument, Alaska, pp. 135-138), and at least four others are known to occur elsewhere in the Monument.

While conducting a floristic survey of Muir Point, a site deglaciated about 1880, I found 11 ferns among the 126 vascular plants, lichens, and mosses comprising the shrub-thicket successional stage. The vegetation on the moraine and outwash deposits here is dominated by Sitka Alder, *Alnus crispa* subsp. *sinuata* (Regel) Hult. The eleven pteridophytes are: *Botrychium lunaria* (L.) Swartz, *Equisetum arvense* L., *E. variegatum* Schleich. subsp. *variegatum, E. variegatum* subsp. *alaskanum* (A. A. Eat.) Hult., *Athyrium filix-femina* subsp. *cyclosorum* (Rupr.) C. Chr., *Cystopteris fragilis* (L.) Bernh. subsp. *fragilis, Dryopteris dilatata* subsp. *americana* (Fisch.) Hult., *Polypodium vulgare* L. subsp. *occidentale* (Hook.) Hult., *Polystichum braunii* subsp. *andersonii* (M. Hopkins) Calder & Taylor, *P. lonchitis* (L.) Roth, and *Woodsia scopulina* D. C. Eat. In addition, the first three named occurred in a strawberry meadow association dominated by *Fragaria chiloensis* subsp. *pacifica* Staudt. This association occurs intermittently along the Muir Point shoreline, depending upon the rate of outward expansion of the Sitka alder thicket, the rate of deposition of new beach material, and the rate of land emergence, which has resulted from the recent loss of the heavy Neoglacial ice load. These three species apparently colonize new physiographic surfaces at this site before the others and persist into the Sitka alder successional stage. Numerous Sitka Spruce, *Picea sitchensis* (Bong.) Carr., protrude above the Sitka Alder thicket and will probably dominate the vegetation within 50 years. Future floristic studies at this site will provide a better understanding of the changing fern flora. Voucher specimens have been deposited in the Herbarium of the University of Minnesota at St. Paul.—*Mark G. Noble, Dept. of Botany, 220 Biological Sciences Center, University of Minnesota, St. Paul, MN 55108.*

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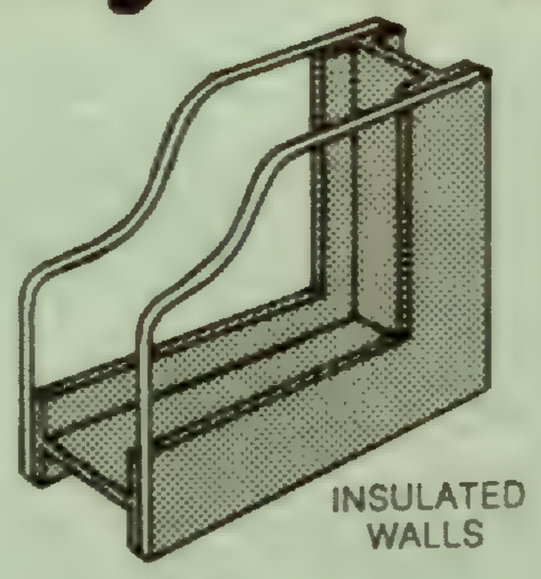

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Re-introduction of Marsilea vestita into Florida

DANIEL B. WARD and DAVID W. HALL*[1]

Any area with a poorly documented flora inevitably accumulates in its list of presumed species an assortment of one-time horticultural escapes, ballast waifs, railroad travelers, agricultural relics, and other chance introductions that are incapable of persistence and hence are not properly full-fledged components of the area's flora. Such plants, once reported, tend to persist in listings long after they have disappeared in the field. Little acclaim is accorded the writer who omits a species that he feels is not adequately documented as a present member of his flora, while a degree of pride and even a measure of competitiveness accompanies the report of a species in an area where it has not previously been known. Thus it is satisfying to provide the first record of *Marsilea* as a current member of the Florida flora since it was reported for the state in the 1890's.

In 1891 L. M. Underwood traveled by rail through Florida, stopping at every opportunity to collect ferns and other vascular plants. In January and in March he paused at a depot known as Orange Bend, in Lake County, central peninsular Florida. Near the depot he found in abundance what he identified as "the *mucronata* form of *Marsilea vestita*." Underwood (1892) published a report of his discovery, noting that his specimens (now at PH, US, YU, and perhaps elsewhere) were the first for this species from east of the Mississippi River.

Guided by Underwood's account, G. V. Nash visited the same location on May 16, 1894. He remarked (1895, p. 161): "The plant occurs along the track on both sides of the depot for about one-quarter of a mile. It is confined to that limited area so far as I could find out. Its occurrence at such a distance from its ordinary range and its limitation to this small section point very strongly to its being introduced." Nash's specimens (PH, US) bear the location "Eustis," but are surely from the Orange Bend station.

A much earlier indication of *Marsilea* in Florida was published by D. C. Eaton (1872), a quarter century before Underwood's report, but has been wholly overlooked by later authors. Eaton possessed a plant from Florida labeled *Marsilea quadrifolia* L. (a European species sparingly introduced into northeastern North America), which he thought "more likely to be one of the western species, *M. uncinata* Braun, for instance." Two sheets in the Eaton herbarium (YU) provide the basis for this brief report. Both are *Marsilea vestita* (and are so annotated by D. S. Correll), and bear the printed label: "Plantae Floridanae: prope Apalachicola [Franklin County], coll. A. W. Chapman, M. D., 1860." Chapman (1897, p. 640), however, acknowledged *Marsilea* in the southeastern United States only near Vicksburg, Mississippi. The labels on the Eaton collections were prepared for his herbarium, and it is possible that an error occurred in the documentation of

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[1]The authors are grateful to the various persons who have assisted us, in loaning specimens, confirming identifications, and in searching for *Marsilea* both in the field and in various herbaria. In particular, we acknowledge the help of O. Lakela, D. B. Lellinger, J. E. Rodman, and E. T. Wherry. This paper is Agricultural Experiment Station Journal Series No. 6109.

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specimens received from Chapman. In any event, if *Marsilea vestita* did occur near Apalachicola, Florida, in 1860, it has not been collected or reported there since and is presumably not at present a member of the flora of panhandle Florida.

It is customary for modern floras such as those of Fernald (1950) and Steyermark (1963) to report Florida within the range of *Marsilea vestita* Hook. & Grev. or of its questionably recognizable segregate, *M. mucronata* A. Br.[2] Small (1931, 1938) reported *Marsilea* for Florida as occurring in "ponds, ditches, and moist places" ("ponds" being of course an invention), and in no way indicated that he had not seen living material from the state and that his entire basis was the Lake County report. Only the cautious C. V. Morton (*in* Gleason, 1952) excluded Florida, although the later condensation by Gleason and Cronquist (1963) restored the unquestioned Florida range. Ward (1968) accepted *Marsilea* for the state. Correll (1938, p. 95) listed *M. vestita* as having been collected in Dade County (*Underwood 66*, PH), as well as in Lake County (*Nash*, PH); this Dade County report, if legitimate, would have been a further range extension, but was not so noted. Wherry (1964) repeated the attribution of *Marsilea* to Dade as well as Lake County, and Lakela and Craighead (1965) again recorded *Marsilea* for Dade County. More recently, Long and Lakela (1971) omitted *Marsilea*. No listing of excluded species was provided, but O. Lakela (pers. comm., 1974) explained that her manuscript was no longer available and conveyed the impression that the omission may have been fortuitous.

Although the Underwood and Nash reports of *Marsilea* in Lake County are documented by collections, the records for its occurrence in Dade County are wholly spurious. The Lakela and Craighead (1965) entry presumably was based on the earlier Wherry and Correll reports. At the request of the senior author, E. T. Wherry re-examined the specimens in the Academy of Natural Sciences upon which both he and Correll had based their reports. He found the Nash collection to be labeled "Eustis," as previously noted. But the other specimen, an Underwood collection of January 1891, was labeled "Orange Beach," a location Wherry assumed was in Dade County. Since there is no such location in Dade County, since Dade County in 1891 was not accessible by rail and was not visited by Underwood, and since Underwood in the same month was collecting *Marsilea* at Orange Bend, Lake County, it is apparent that the Dade County reports were based upon a misinterpreted (and uncritically copied) Lake County collection.

In April 1962, the senior author, with members of a University of Florida taxonomy class, made an effort to relocate the Underwood and Nash *Marsilea* station in Lake County. By the use of 1890 railroad maps and by local inquiry, the site of the Orange Bend depot was located, and has since been confirmed by a modern topographic map (U. S. Geol. Surv. Leesburg East, 1965). The long-since-destroyed depot once stood about one mile northwest of the present Orange Bend, a hamlet just south of the larger town of Lisbon. Remnants of the depot foundation alongside the Florida Coast Line tracks were still visible in 1962. But

[2]The view that *M. mucronata* A. Br. merited specific segregation from the older *M. vestita* Hook. & Grev. can be traced to C. A. Weatherby (*in* Johnston, 1943); the only consequential modern contrary opinion is that of Cronquist (1972, p. 220).

the adjacent ditch where Underwood and Nash had collected was largely filled with dry cinders, and no *Marsilea* could be located.

In the years since 1962, *Marsilea* has seemed destined for footnote status in any future Flora of Florida. In September 1975, however, fragmentary plants of *Marsilea* were sent to the Agricultural Experiment Station, University of Florida, with the request that they be identified and that control measures be recommended. This led to a collection made on 25 Sept 1975 from a very extensive stand on the moist to dry soil of lawns and flower beds in a residential area ninety miles southwest of the Orange Bend station: 1400 block, West College Avenue, Ruskin, Hillsborough County, Florida (*D. W. Hall 414*, FLAS (2), FSU, GA, GH, NY, PH, US, YU). The plants, although sterile, were identified tentatively by D. B. Lellinger as typical *M. vestita* Hook. & Grev. Residents in the area of the Ruskin station were of the opinion that the *Marsilea* had its origin in 1970 as an accidental inclusion with garden plantings brought from New Orleans. At first they were intrigued by its four-lobed "lucky clover" leaves, but more recently have found it to be a persistent and rapidly spreading weed.

Marsilea vestita thus is again definitely known in Florida, and its disappearance now seems unlikely. It appears that this western species, still, as in Nash's day, scarcely known east of the Mississippi River, may have passed from the status of a rare plant, through the limbo of a long-uncollected species, to become a botanical novelty of negative economic worth.

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Diplazium delitescens and the Neotropical Species of Asplenium sect. Hymenasplenium

ALAN R. SMITH*

Since the original description of *Diplazium delitescens* Maxon, no one has seriously questioned its generic disposition. However, a preliminary study of herbarium material of this uncommon neotropical species suggests that it might be better placed in *Asplenium*. Maxon relied chiefly on the back-to-back arrangement of linear sori in ascribing this species to *Diplazium*. In contrast, spleenworts generally have only single, linear sori on the ultimate veins. Although soral arrangement is the primary (and usually most reliable) character used to separate the two genera, I report here a survey of additional characters that provide good evidence for transferring *D. delitescens* to *Asplenium*.

Sporangia.—The species of *Asplenium* consistently have one-rowed sporangial stalks, at least at the base (Bower, 1928, p. 140; Tardieu-Blot, 1932, p. 363) and sporangial capsules that often split divaricately at the tip of the fully extended or backwardly flexed annulus. *Diplazium delitescens* possesses both these characteristics (*Fig. 1*). Other species of *Diplazium* have shorter, two- or three-rowed sporangial stalks, with annuli often not extended and capsules not splitting divaricately at the tip, e.g., *D. werckleanum* Christ (*Fig. 2*). I have been unable to find any reference to this distinctive type of sporangial opening in *Asplenium*, but I believe it may be a very useful character in distinguishing asplenioid species from other groups of ferns.

The number of annular cells in *Asplenium* is generally higher than in *Diplazium*. Tardieu-Blot (1932, p. 364) reported 15-20 annular cells for species of *Diplazium* and 20-25 annular cells for species of *Asplenium*. Copeland (1947, p. 147) listed *Diplazium* (in *Athyrium*) as having an "annulus of 12-20 (commonly 16) thickened cells," whereas *Asplenium* was described as having an "annulus usually of 20-28 cells." I have made five counts each on *A. laetum* Swartz (*Breedlove 33893*, DS), *A. abscissum* Willd. (*Breedlove 22178*, DS), *A. harpeodes* Kunze (*Breedlove 22504*, DS), and *A. auriculatum* Swartz (*Breedlove 22506*, DS); these species averaged 23, 20, 21, and 20 annulus cells per sporangium, respectively. *Diplazium franconis* Liebm. (*Breedlove 22421*, DS), *D. lonchophyllum* Kunze (*Breedlove 22461*, DS), *D. acutale* Fée (*Breedlove 22760*, DS), and *D. werckleanum* Christ (*Breedlove 33664*, DS) all averaged 15 annular cells per sporangium. *Diplazium delitescens* (*Breedlove 33853*, DS) averaged 21 annular cells per sporangium, which agrees with *Asplenium*.

Spores.—*Diplazium delitescens* spores have numerous, sharp folds in the perispore (*Fig. 3*), and are similar to, or even indistinguishable from, spores of several species of *Asplenium* from southern Mexico and Central America, e.g., *A.*

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auriculatum (*Fig. 4*), *A. laetum*, *A. abscissum*, and *A. harpeodes* (vouchers the same as listed above). On the other hand, *Diplazium* spores tend to have a loosely folded perispore without sharp ridges, e.g., *D. werckleanum* (*Fig. 5*), *D. acutale*, *D. lonchophyllum*, and *D. franconis* (vouchers the same as listed above). Although there is considerable variation in perispore morphology in both *Asplenium* and *Diplazium*, these spore characterizations are in general agreement with the illustrations of spores of the two genera in Tardieu-Blot (1932, pl. 49 and 50), Wagner (1952, pl. 5), Erdtman (1957), Nayar and Devi (1963), Nayar (1964), and Tschudy and Tschudy (1965).

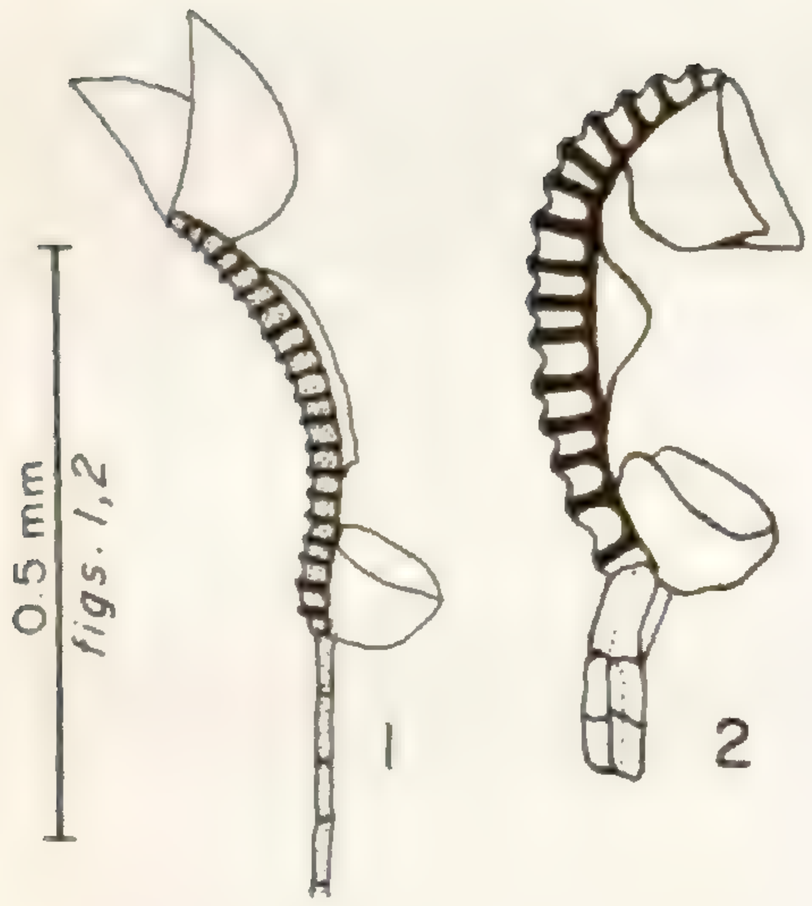
Sori.—*Diplazium delitescens* has both single sori, which is typical of *Asplenium*, and sori paired back-to-back, which is found generally throughout *Diplazium*.

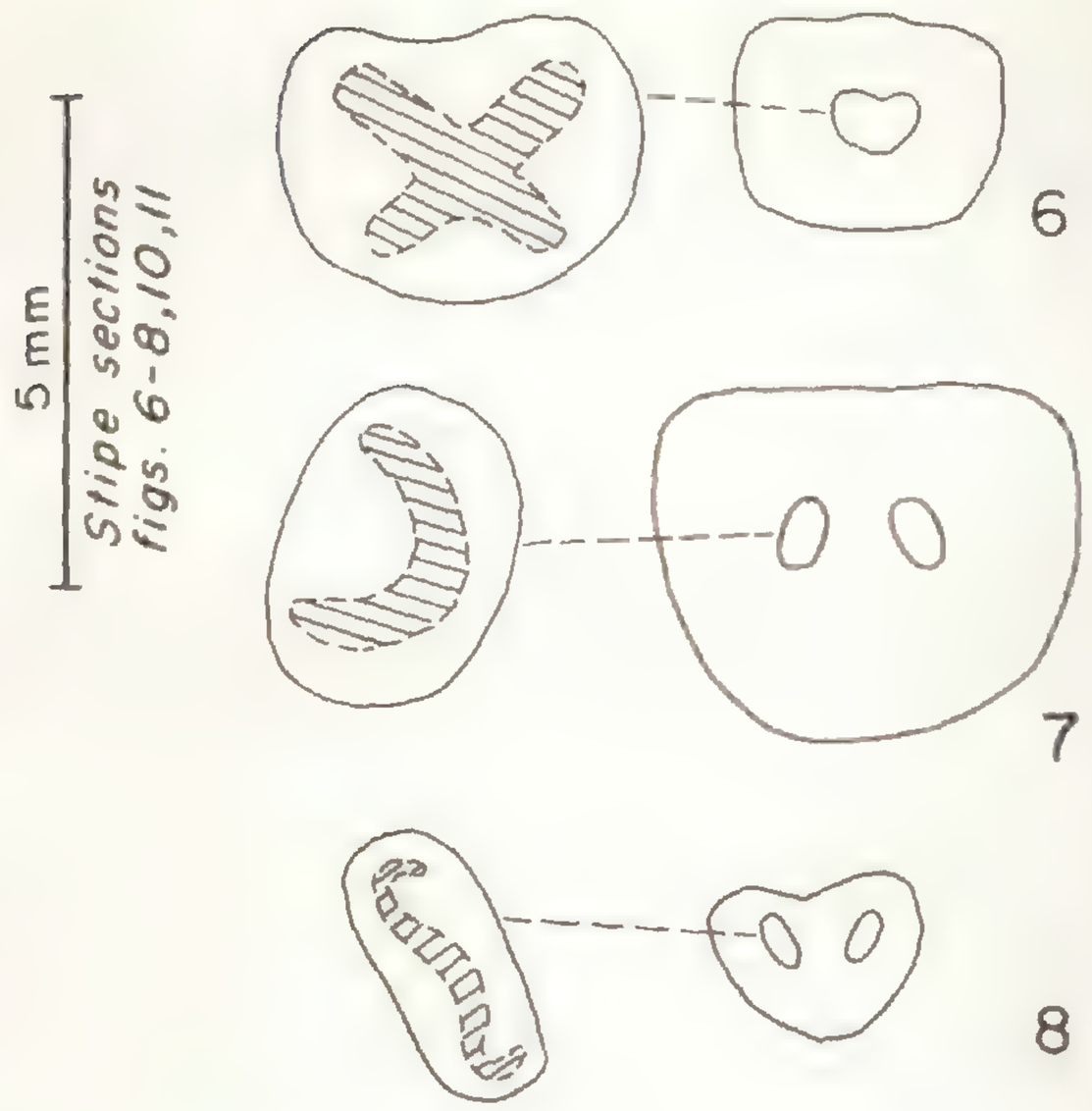
Rhizome habit.—The creeping rhizome of *D. delitescens* is aberrant when compared with the suberect to erect rhizomes of other neotropical *Diplazium* species. Repent rhizomes are also unusual in *Asplenium*, but do occur in a few species, namely, *A. obtusifolium* L., *A. repandulum* Kunze, *A. hoffmannii* Hieron. (syn. *A. membranifolium* Maxon), *A. melanopus* Sod., and *A. laetum* Swartz, as well as the Old World species belonging to *Asplenium* sect. *Hymenasplenium* (Hayata) K. Iwats. (Iwatsuki, 1975). According to Iwatsuki, this section comprises five Old World species (*A. unilaterale* Lam., *A. excisum* Presl, *A. subnormale* Copel., *A. obscurum* Blume, and *A. cheilosorum* Kunze ex Mett.) and possibly a few New World ones. Iwatsuki believes that the dorsiventral rhizomes of sect. *Hymenasplenium* are an adaptation to a rocky habitat. Most of these Old World species grow on wet rocks adjacent to or even in streams; the one exception appears to be *A. excisum*, which Iwatsuki believes to grow terrestrially on rich humus in deep forest.

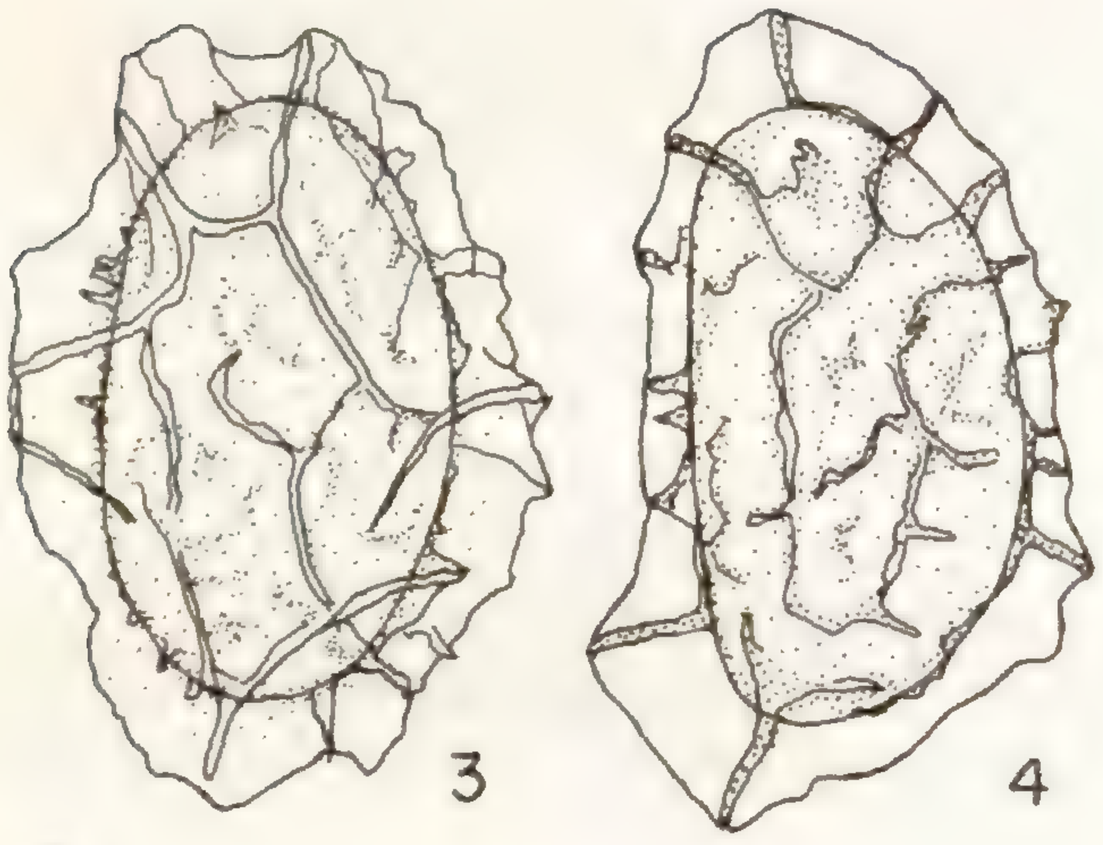
The habitat favored by several neotropical species of *Asplenium* with creeping rhizomes also appears to be wet rocks adjacent to or within streams. This is certainly true of *A. obtusifolium* and *A. repandulum*, at least in southern Mexico; see Morton and Lellinger, (1966, p. 12) for a somewhat different opinion. *Asplenium melanopus* has been recorded as "among rocks of streambed" (*Mexia 6223*, UC). *Asplenium laetum* and *A. hoffmannii* are apparently terrestrial or on wet rocks often near, but not within, streams. Precise habitat information is not yet available for *D. delitescens*.

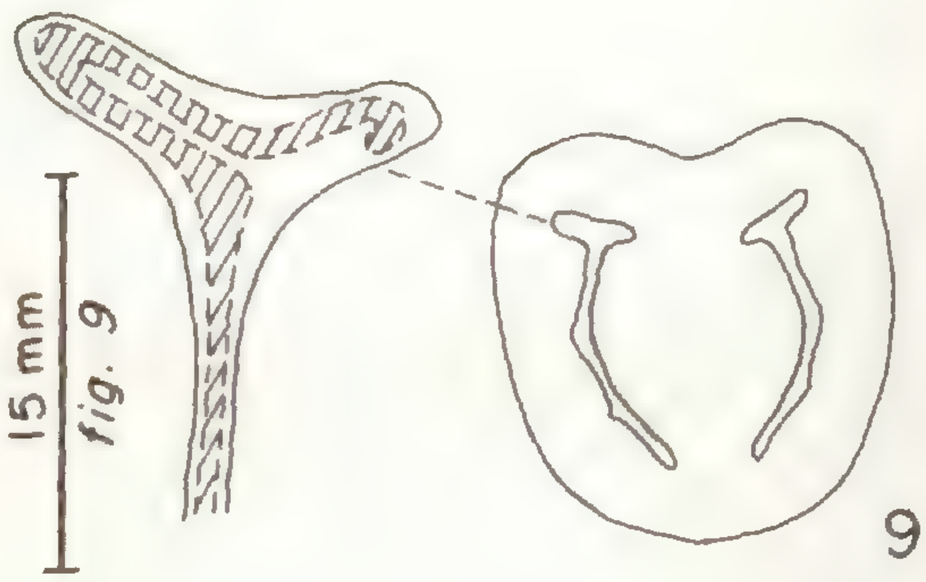
Phyllopodia.—The species of *Diplazium* lack phyllopodia. *Diplazium delitescens*, like some species of *Asplenium*, has phyllopodia.

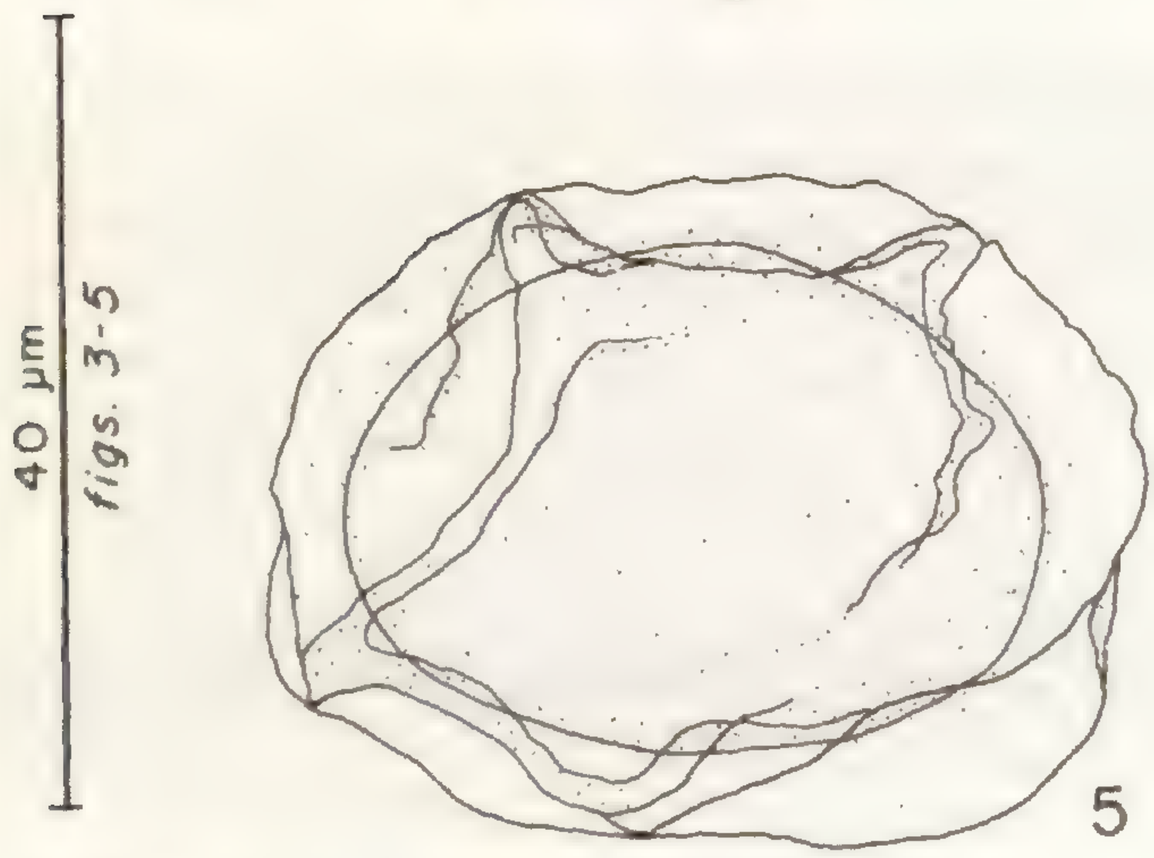
Stipe vasculature.—*Asplenium* and related genera, e.g., *Diellia* and *Camptosorus*, characteristically have two traces from the rhizome stele leading to the base of the stipe which are elliptical in cross-section; each of these meristeles contains a xylem strand that is C-shaped in cross-section. These two traces may unite in the cortex of the rhizome (below the stipe), in the stipe base, or midway up the stipe to form a distinctive xylem strand that is X-shaped in cross-section (Ogura, 1972; Bir, 1970; Wagner, 1952, p. 82; Tardieu-Blot, 1932, pl. 40-42). Among neotropical species, I find this familiar X-shaped vascular pattern in the stipe bases of *A. tuerckheimii* Maxon (*Fig. 6*), *A. abscissum* Willd. (*Bourgeau s. n.*,

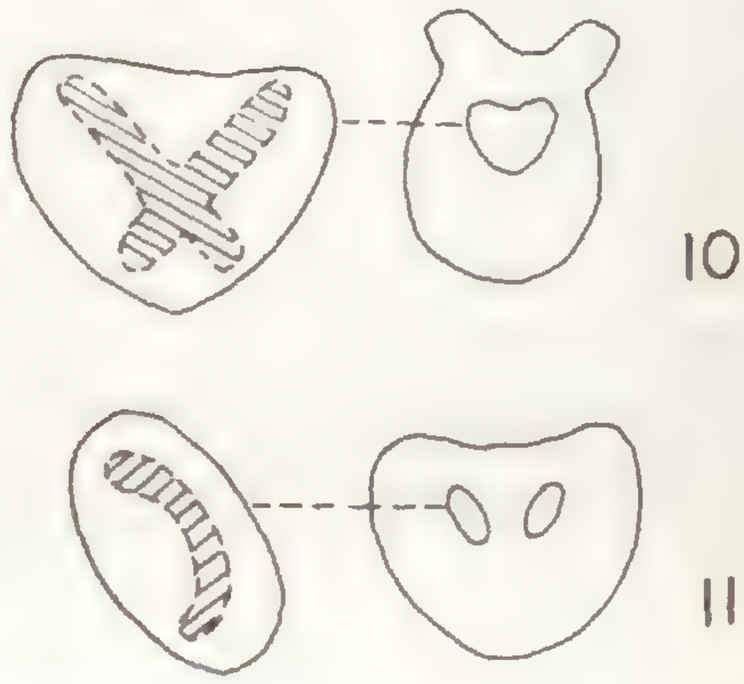












Sporangia, spores, and stipe cross-sections in *Diplazium* and *Asplenium*. FIG. 1. Open sporangium of *D. delitescens* (*Breedlove 33853*, DS). FIG. 2. Same, *D. werckleanum* (*Breedlove 33672*, DS). FIG. 3. Spore of *D. delitescens* (*Breedlove 33853*, DS). FIG. 4. Same, *A. auriculatum* (*Breedlove 22506*, DS). FIG. 5. Same, *D. werckleanum* (*Breedlove 33672*, DS). FIG. 6. Cross-section of stipe base in *A. tuerckheimii*, with enlargement of meristele (*Purpus 6432*, UC). FIG. 7. Same, *A. achilleifolium* (*Carlson 417*, UC). FIG. 8. Same, *D. ternatum* (*Breedlove 32387*, DS). FIG. 9. Same, *D.* cf. *pinnatifidum*, with enlargement of portion of meristele (*Mickel 3064*, NY). FIG. 10. Cross-section of stipe near blade base in *D. delitescens*, with enlargement of meristele (*Breedlove 29935*, DS). FIG. 11. Cross-section of stipe base in *D. delitescens*, with enlargement of meristele (*Breedlove 22482*, DS).

UC), *A. cristatum* Lam. (*Chrysler 5143*, UC), and *A. harpeodes* Kunze (*Papenfuss s.n.*, UC). Species possessing two meristeles (each with a C-shaped vascular pattern) at the stipe base are *A. achilleifolium* (Mart. & Gal.) Liebm. (*Fig. 7*), *A. auritum* Swartz (*Gentle 6661*, UC), *A. oligophyllum* Kaulf. (*Hutchison 1485*, UC), and *A. feei* Kunze (*Purpus 7110*, UC). In addition, all the Asian species I examined of *Asplenium* sect. *Hymenasplenium*, which included *A. obscurum* (*Rodin 8128*, UC), *A. excisum* (*A. C. Smith 5783*, UC), *A. subnormale* (*Sachalian s.n.*, UC), and *A. cheilosorum* (*Copeland 163*, UC), have in cross-section two elliptic meristeles with C-shaped strands in the stipe base.

The species of *Diplazium*, like those of *Asplenium*, usually have two vascular strands in the stipe bases; these strands remain separate for most of the stipe length, but towards the apex unite to form a bundle that is gutter- or U-shaped in cross-section (Ogura, 1972; Bir, 1962; Tardieu-Blot, 1932, pl. 36 and 37). On the other hand, the X-shaped xylem patterns of *Diplazium*, unlike those of *Asplenium*, have pronounced hooks at their adaxial ends and, to a lesser extent, at their abaxial ends (the hippocampus-shaped bundles of Ogura, 1972). I have observed hippocampus-shaped xylem strands in the following New World species: *D. ternatum* Liebm. (*Fig. 8*), *D.* cf. *pinnatifidum* Kunze (*Fig. 9*), *D. obscurum* Christ (*Mickel 3010*, NY), *D. seemannii* Moore (syn. *D. macrotis* (Baker) Christ, *Mickel 3062*, NY), *D. lonchophyllum* Kunze (*Mickel 2968*, NY), *D. plantaginifolium* (L.) Urban (*Breedlove 31507*, DS), and *D. werckleanum* (*Breedlove 26827*, DS). These strands apparently never have the back-to-back-C arrangement characteristic of the *Asplenium* vascular pattern. The larger species of *Diplazium* tend to have somewhat more elaborate strands (Bir, 1969). However, differences in stipe vasculature are not simply a function of stipe size, for the stipes of *D. ternatum* and *D. plantaginifolium* have a smaller diameter than do those of many *Asplenium* species examined in this study.

Stipe vasculature in *D. delitescens* is much more like that in *Asplenium* than that in *Diplazium*, and matches closely the vasculature of species belonging to *Asplenium* sect. *Hymenasplenium:* two elliptical bundles fuse high in the stipe to give the asplenioid X-pattern (*Figs. 10* and *11*).

Rhizome scales.—In general, *Asplenium* is characterized by having clathrate scales, with dark, lateral walls and clear, often transparent lumina; in *Diplazium*, the lumina show little contrast with the lateral walls, and are usually brownish, apparently never transparent (Tardieu-Blot, 1932, p. 357). The stipe base scales of *D. delitescens* are clearly clathrate, although this condition is not so obvious as in many spleenworts because the scales are few, narrow, and often dirt-covered. The lumina are nearly transparent, with thick and dark lateral walls.

Chromosome number.—Chromosome number should provide a means of placing *D. delitescens*. Nearly all *Asplenium* species have a base number of $x=36$, with *A. unilaterale* (sect. *Hymenasplenium*) counted several times as $n=40$. The only count available for a New World *Asplenium* with a creeping rhizome is $n=36$ for *A. laetum*. *Diplazium* species consistently have $x=41$.

On the basis of the aforementioned characters, I believe that *D. delitescens* is best treated as a member of *Asplenium*, probably most closely related to species in

sect. *Hymenasplenium* (Hayata) Iwatsuki:

Asplenium delitescens (Maxon) A. Reid Smith, comb. nov.

Diplazium delitescens Maxon, Contr. U. S. Nat. Herb. **10**: 497. 1908. TYPE: Vicinity of S. Luis, Pcia. Oriente, Cuba, *Pollard & Palmer 348* (US).

The neotropical species of *Asplenium* sect. *Hymenasplenium* appear to be: *A. delitescens, A. hoffmannii, A. laetum, A. melanopus, A. obtusifolium,* and *A. repandulum. Asplenium melanopus,* known from Colombia to Peru, has often been treated as *Diplazium melanopus* (Sod.) Hieron., but was first described in a broadly circumscribed *Asplenium* that included *Diplazium. Asplenium melanopus* appears to be most closely related to *A. laetum,* but it may also have affinities to *A. delitescens.* Another species of this group may be *Asplenium purpurascens* Mett. ex Kuhn, based on a type from Ecuador, which is described as having a creeping rhizome; I have seen too little material to place it here with certainty.

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Diffusive Resistance, Titratable Acidity, and CO_2 Fixation in Two Tropical Epiphytic Ferns

S. C. WONG and C. S. HEW*

Crassulacean acid metabolism (CAM) is known to occur in many succulent plant species (Ranson & Thomas 1960; Ting et al., 1972; Wolf, 1960). To date, more than 184 plant species have been reported to exhibit CAM features, but none of them are ferns (Szarek, pers. comm.). Recently we reported nocturnal assimilation of CO_2 by *Drymoglossum piloselloides* (L.) Presl, an epiphytic fern (Hew & Wong, 1974). This paper presents further evidence to support our previous findings that certain epiphytic ferns do exhibit characteristics of CAM plants.

Two epiphytic ferns, *Pyrrosia longifolia* (Burm.) Morton and *Drymoglossum piloselloides,* were chosen for the present investigation. These ferns are found frequently on the lower part of *Acacia* tree trunks. *Gleichenia linearis* (Burm.) Clarke, a terrestial sun fern which has been shown to be a C_3 plant (Hew & Wong, 1974), also was included in the study. All three ferns grow wild around the Nanyang University campus. For comparison purposes, the flowering plant *Kalanchoë pinnata,* a known CAM plant, was also used as experimental material.

For $^{14}CO_2$ fixation studies and determination of titratable acidity, detached leaves or fronds were used; the method for $^{14}CO_2$ fixation has been described previously (Wong & Hew, 1973). Titratable acidity of plant tissues was determined as described by Szarek and Ting (1974), except the leaf or frond extract was titrated to a $pH_7\uparrow$ end point. Diffusive resistance of intact fronds or leaves were measured at three hour intervals using an Li-60 Diffusive Resistance Meter (Li-Cor Limited).

Titratable Acidity.—The diurnal changes in titratable acidity of *Drymoglossum, Pyrrosia,* and *Kalanchoë* were similar (*Figs. 1-3*). Titratable acidity decreased in the light, and at night the acidity increased. The magnitude of dark acidification in these three species was comparable to that previously reported (Bruinsma, 1958; McWilliams, 1970; Szarek & Ting, 1974). Among the three species, titratable acidity was highest in *Kalanchoë*, both in light and darkness. There was no significant difference in titratable acidity between the two ferns. In contrast, *Gleichenia* (*Fig. 4*), which is a C_3 plant, shows no diurnal fluctuation in titratable acidity.

Diffusive Resistance.—Changes in diffusive resistance patterns of intact *Pyrrosia* fronds (*Fig. 5*) and *Kalanchoë* leaves (*Fig. 6*) in the day and at night were similar, with high diffusive resistance in the day and low at night. The values for minimum diffusive resistance (5-15 $sec \cdot cm^{-1}$) and maximum diffusive resistance (100-120 $sec \cdot cm^{-1}$) also were in agreement with that of other succulent plants (Szarek & Ting, 1974; Ting et al., 1972). From the changes in patterns, one could conclude that *Pyrrosia* and *Drymoglossum* stomata were closed in the day and open at night (Nishida, 1963; Ting et al., 1972). A point worth noting is that with the onset of darkness, an increase in diffusive resistance in both *Pyrrosia* and

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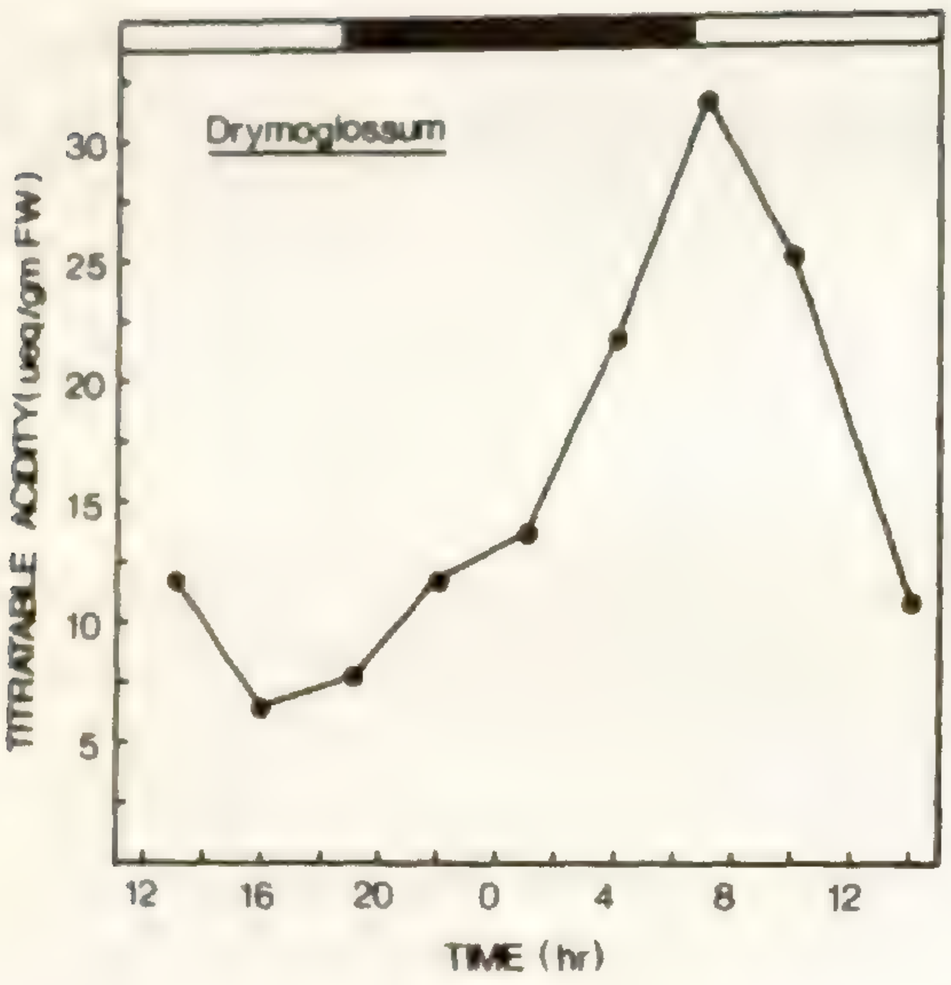

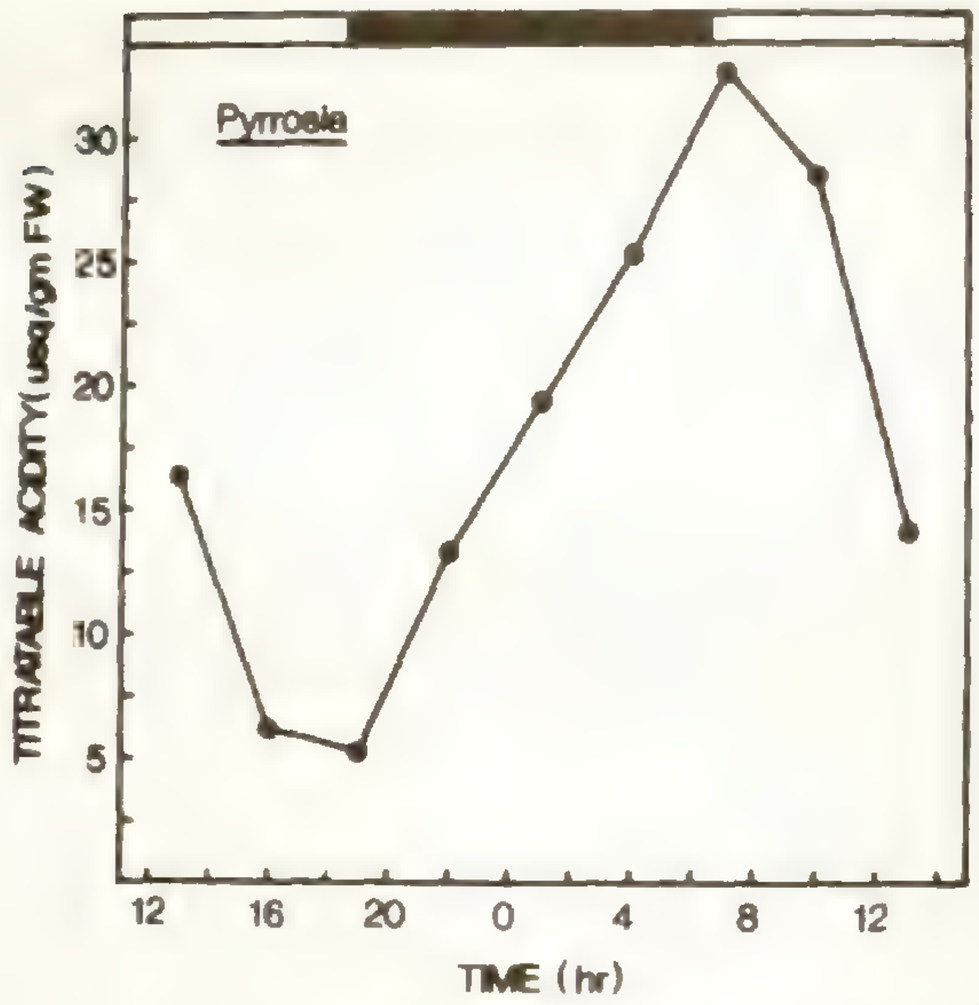

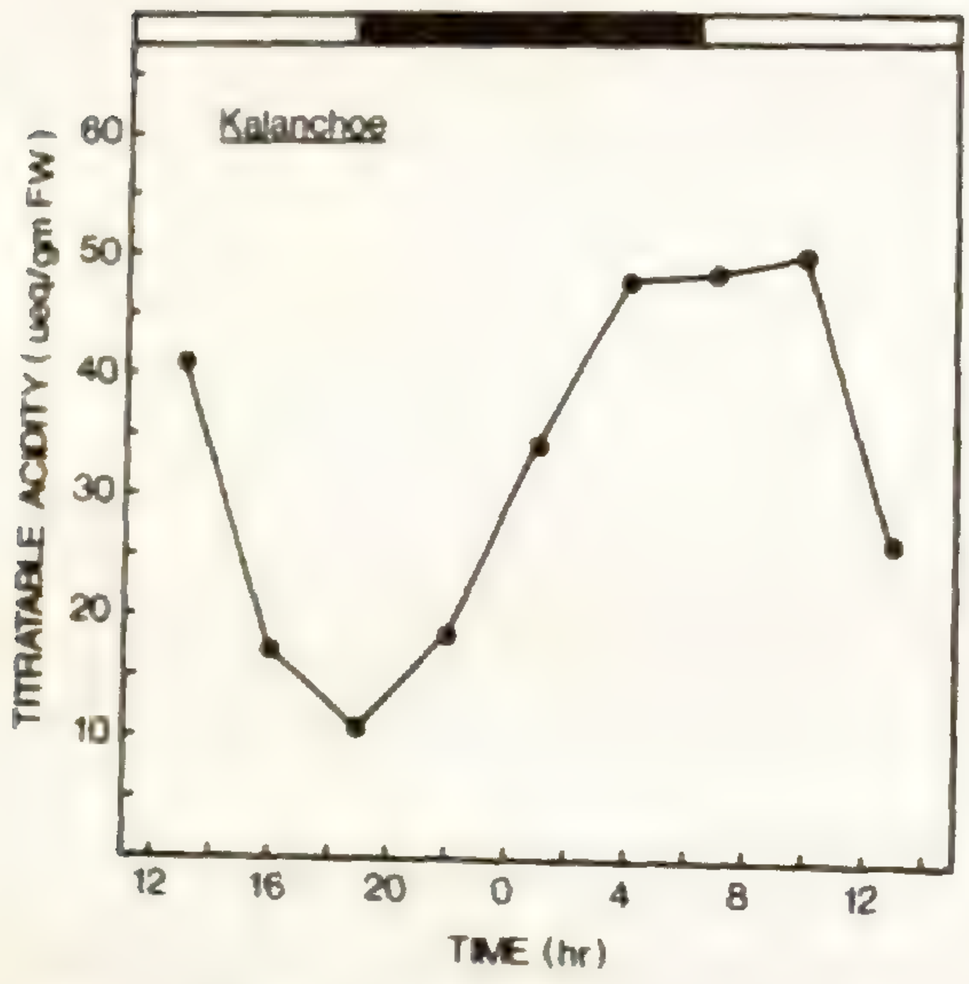

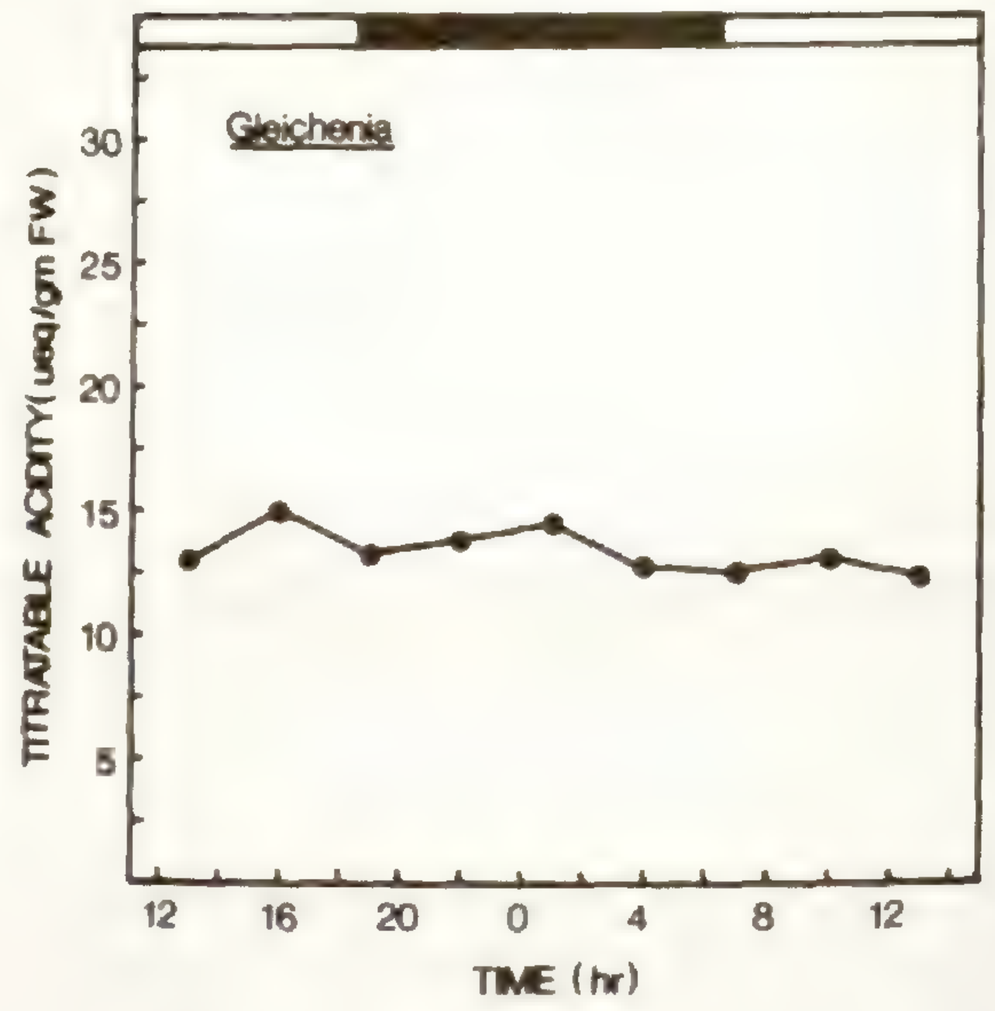

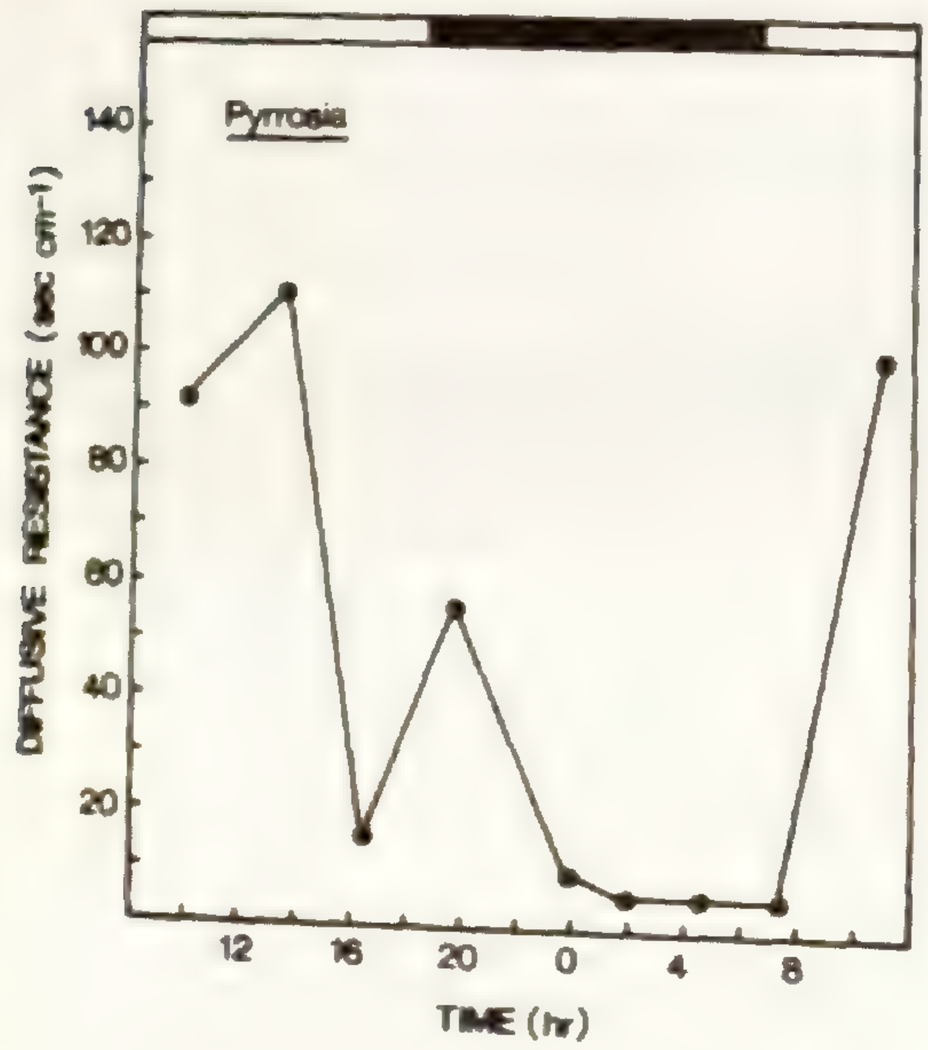

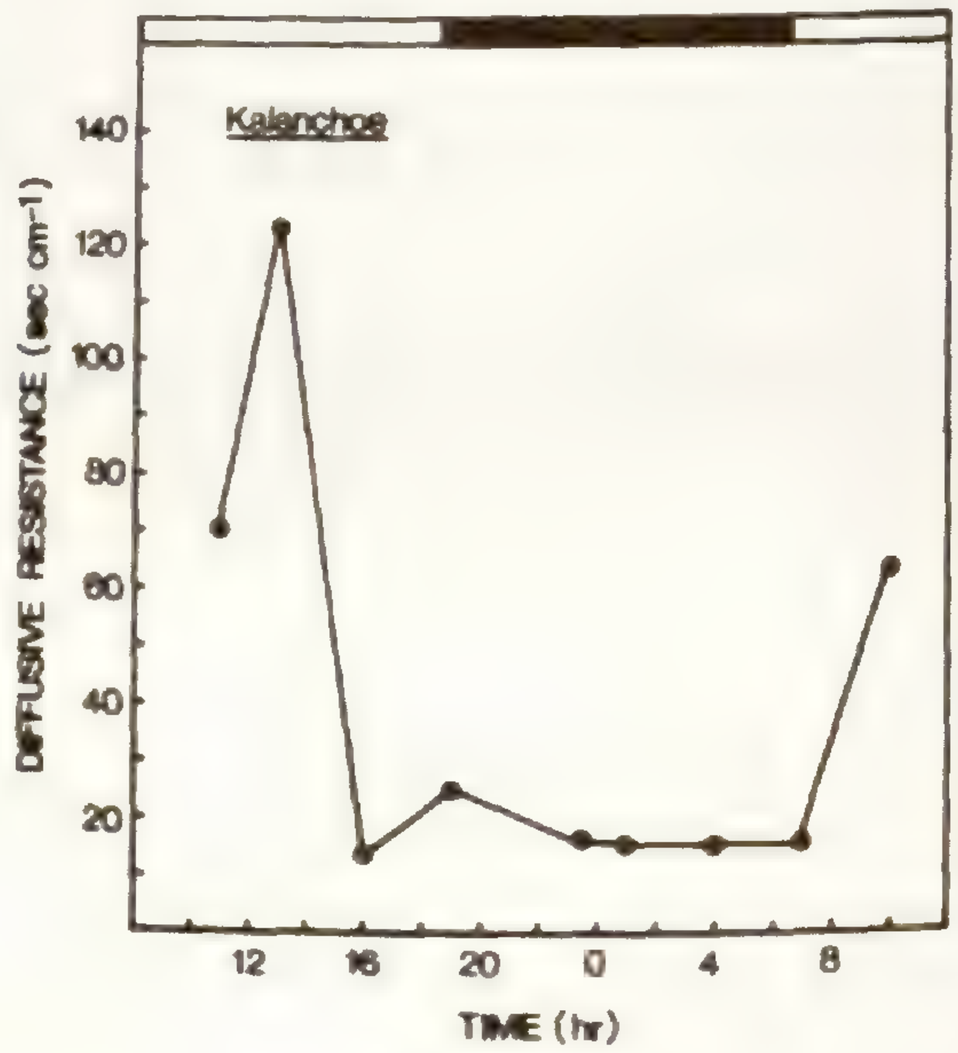

FIGS. 1-4. Diurnal changes in titratable acidity of *Drymoglossum*, *Pyrrosia*, *Kalanchoë*, and *Gleichenia*. FIGS. 5-6. Diurnal changes in diffusive resistance of *Pyrrosia* and *Kalanchoë*.

Kalanchoë was observed (*Figs. 5-6*). This increase in resistance probably could account for the rapid decrease in CO_2 uptake by thick-leaved orchids when light was turned off suddenly during the course of CO_2 gas exchange determination (Hew, 1976; Wong, 1973).

$^{14}CO_2$ Fixation.—To ascertain the nature of dark acidification in ferns, *Pyrrosia* and *Drymoglossum* fronds were harvested at 3 p.m. and were allowed to fix $^{14}CO_2$ in darkness for various lengths of time. Malate was the only product labelled with radioactive carbon in a short term fixation experiment. The increase in titratable acidity in *Pyrrosia* and *Drymoglossum*, therefore, was due to a massive accumulation of malate, as has been observed in other CAM plants (Bradbeer et al., 1958; Cockburn & McAulay, 1975; McWilliams, 1970; Ranson & Thomas, 1960; Sutton & Osmond, 1972; Ting et al., 1972).

Pyrrosia and *Drymoglossum* are two of the very common tropical epiphytic ferns of exposed or moderately exposed places in Singapore. These ferns are, in fact, closely related (Holttum, 1954). The fronds are fleshy and contain special layers of water storage cells. Also, the lower surface of the frond of both species is covered with stellate hairs, which prevents excessive water loss (Holttum, 1954). As in other plants (Hew, 1976; McWilliams, 1970; Neales et al., 1968; Neales & Hew, 1975; Ting et al., 1972), structural adaptations in ferns are accompanied by physiological changes. From the diurnal changes in diffusive resistance, titratable acidity, and CO_2 fixation, we conclude that *Pyrrosia* and *Drymoglossum* are CAM plants.

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Comparative Studies in the Biology of Lycopodium carolinianum

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Lycopodium carolinianum L., both temperate and tropical in distribution, occurs in North America along the Gulf and Atlantic coasts as far west as Texas and as far north as Long Island, New York. Its green, surficial gametophytes were described by Koster (1941), and Löve and Löve (1958) reported a chromosome number for it of $n=39$. Various authors have included the species in morphological or anatomical surveys of the genus, but little concerted effort has been given to a detailed study (Wilce, 1972; Chu, 1974; Øllgaard, 1975; Bruce, 1976). Ballard (1950), in his work on African *L. carolinianum*, has produced the most complete study to date.

Taxonomically, several authors have treated the plant. Baker (1887, p. 28) aligned *L. carolinianum* with his subg. *Diphasium* on the basis of its distichous, dimorphous leaves. Most authors now relate it to subg. *Lepidotis, sensu* Wilce (1972). The latter association is based on habit, chromosome number, external spore morphology, and type of gametophyte. However, in confirming certain chromosome numbers in subg. *Lepidotis*, it was found that *L. carolinianum* had a number different from that reported by Löve and Löve (1958), viz. $n=35$ (Bruce, 1974). In addition, the structure of its strobilus and peduncle is different from the general condition of subg. *Lepidotis* and is like that in subg. *Lycopodium*. The latter group includes such species as *L. clavatum* L. and *L. complanatum* L. Consequently, studies were undertaken to circumscribe *L. carolinianum* both morphologically and anatomically in a more complete manner and through this to assess its relationships within the Lycopodiaceae.

MATERIALS AND METHODS

Field data from 25 localities were collected from New Jersey south and west along the coastal plain to Louisiana. Materials were preserved in FAA, FPA, or CRAF IV for anatomical preparations. Microtome sections were prepared of seven strobili, five peduncles, 12 rhizomes, and five roots. Paraffin technique was employed and sections were cut 8-15 μm in thick. These were then stained using Sharman's (1943) technique or safranin-fast green (Johansen, 1940, p. 80). Cytological material was placed into a saturated, cold, aqueous solution of paradichlorobenzene and transferred (usually after an hour) to Newcomer's solution (Newcomer, 1953) at room temperature. The vial containing the Newcomer's solution and cytological material was then transferred after an hour into a freezer until examined. The chromosomes were prepared by the squash technique and were mounted in and stained by a 1:1 solution of Hoyer's mounting medium (Beeks, 1955) and acetocarmine. The preparations were made permanent by ring-

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FIGS. 1-6. *Lycopodium carolinianum*. FIG. 1. Habit, × ¼. FIG. 2. Phyllotactic patterns based upon the number of dorsal ranks of leaves. Pattern to left shows anisodichotomous branching, × 1.2. FIG. 3. Mature rhizome transection, × 36. FIG. 4. Rhizome tubers showing variation in shape and branching, × 1.8. FIG. 5. Mature tuber transection, stele apparent as dark region in center, × 24. FIG. 6. Longisection of mature tuber; the darker portion of the cortex is due to starch, × 6.5.

ing the coverslip with clear fingernail polish. Dr. F. S. Wagner, University of Michigan, originally worked out this cytological technique. Photographs of both anatomical sections and cytological preparations were made on Panatomic-X film with a Zeiss Standard WL research microscope or on Tri-X or Ektapan sheet film with an Aristophot 4×5 view camera. In addition, herbarium material of *L. meridionale* Underw. & Lloyd was examined and anatomical preparations were made using Schmid's (1971, p. 13) technique.

RESULTS

Habit and habitat.—*Lycopodium carolinianum* occurs in the United States in grassy, sandy habitats along with members of the *L. alopecuroides* L. complex of subg. *Lepidotis* (*Fig. 1*). The most prolific development is found in open, sandy, damp borrow pits, and more or less open, broad, sandy ditches along roads.

The photosynthetic portion of the sporophyte is a prostrate shoot which branches anisodichotomously (*Figs. 1* and *2*). The single strobilus develops atop a thin, elongate peduncle which possesses scattered, reduced leaves (*Figs. 16* and *17*). Many plants are sterile and produce no strobili. New plants are formed vegetatively as the older rhizome parts decay, thereby breaking organic connection between branch shoots.

Rhizomes.—The phyllotaxy of the rhizome of *L. carolinianum* reveals three distinct patterns (*Fig. 2*). Two lateral ranks of broad based leaves occur so that the leading edge of one leaf underlies the trailing edge of the leaf next closest to the apex. These lateral leaves are arranged in approximate pairs. Dorsally, along the top of the stem, there may be one, two, or three ranks of smaller leaves corresponding to the three patterns. Vascular traces to the lateral leaves depart from the stele essentially parallel to the ground in all three phyllotactic types. The lateral ranks of leaves are displaced differentially depending upon the phyllotactic pattern.

The leaf primordia in the shoot apex are not all of the same size initially. The primordia of the two lateral ranks of leaves are largest and involve much of the lateral flanks of the meristematic tip. The spiral phyllotaxy, characteristic of *Lycopodium* in general, is here greatly distorted.

The mature stem consists of a central stele surrounded by a three-zoned cortex and epidermis (*Fig. 3*). The stele is moderately banded and surrounded by a narrow, parenchymatous cortical zone. Surrounding this parenchymatous layer is a sclerenchymatous band 3 or 4 cells thick. The bulk of the stem is composed of the large-celled parenchymatous outer cortex whose peripheral layers are chlorophyllous. A single-layered epidermis bounds the cortex. The leaves have a single, unbranched mesarch vascular strand which lacks phloem. The leaves are uniformly parenchymatous, and their cells are elongate parallel to the vein.

Tubers.—Rhizome tips may form underground, perenniating tubers in late fall (*Fig. 4*). In spring, the storage shoot grows to the soil surface, whereupon normal plagiotropic growth resumes. The frequency of tuber formation is relatively low. In two collections totaling 391 shoot tips, tubers were present on 18/179 (10.0%) shoot tips of one collection and 13/212 (6.1%) of the other.

Mature roots of *L. carolinianum* possess a distinctive internal structure (*Fig. 13*). The stele is typical of most *Lycopodium* roots with its C-shaped xylem strand. A three or four cell thick layer of thin-walled cells immediately surrounds the stele in mature roots. External to this inner cortical layer is a large, cylindrical lacuna (*Figs. 10* and *13*). When mature roots are placed under water, this air filled cavity is obvious through the outer cell layers. Developing roots initially have several thin-walled layers where the lacuna forms. Although air can be seen within the root often to 0.5 mm of the tip, it is due to the large intercellular spaces in the thin-walled cell zone of the cortex prior to the formation of the lacuna. At about 1.0 cm from the root tip, these cells begin to separate from each other and collapse, and the conspicuous, empty ring in the cortex of older roots becomes apparent approximately 1.0 mm from the site of the initial degeneration. Peripheral to the lacuna is the outer cortex, which is two or three cells wide. The cells of the outer cortex have thicker walls than those of the inner cortex. An epidermis is present which is not much differentiated from the outer cortex, but which produces the root hairs.

The root hairs are thin cells which protrude perpendicularly to the root axis. They are nucleate, nonseptate, and usually paired (*Figs. 11* and *15*). Maximum length was not determined, although there were many in excess of 1.0 mm.

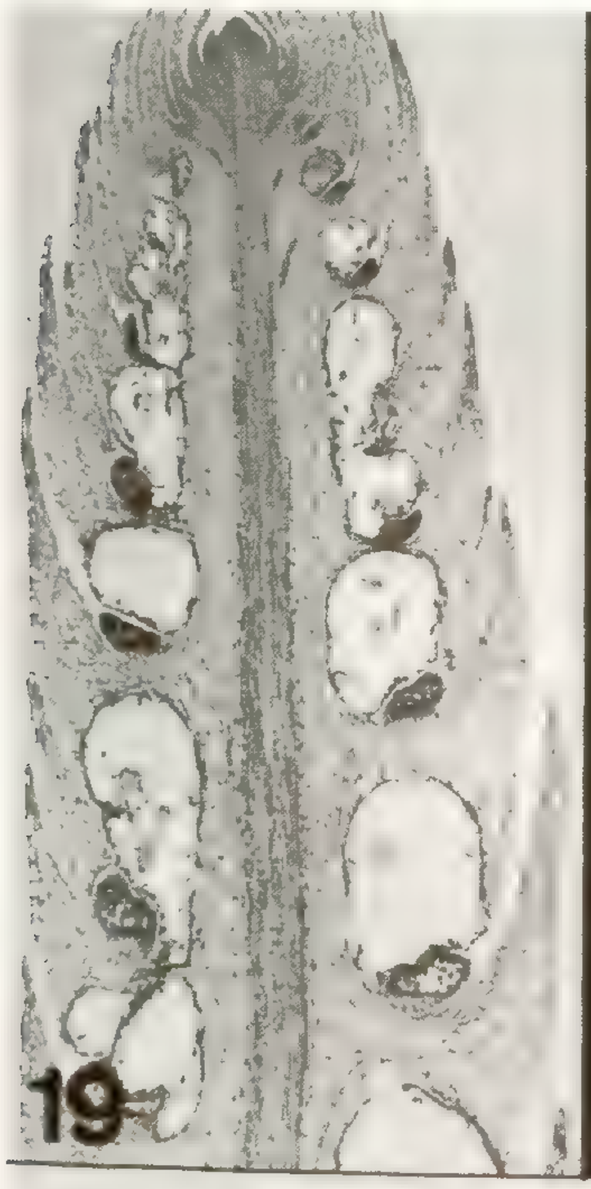
The cells of the root protoderm are produced in longitudinal files extending from near the root tip. Every other cell in the file subsequently elongates and forms a tabular cell of the root epidermis (*Fig. 11*). The remaining cells usually undergo an anticlinal division parallel to the line of the file. This produces two initials which then elongate perpendicularly to the root axis to form paired root hairs (*Fig. 15*, arrows). First evidence of root hair growth is seen approximately 0.5 mm from the tip; when the root hairs are 1.5 mm from the root tip, they are apparently fully elongate.

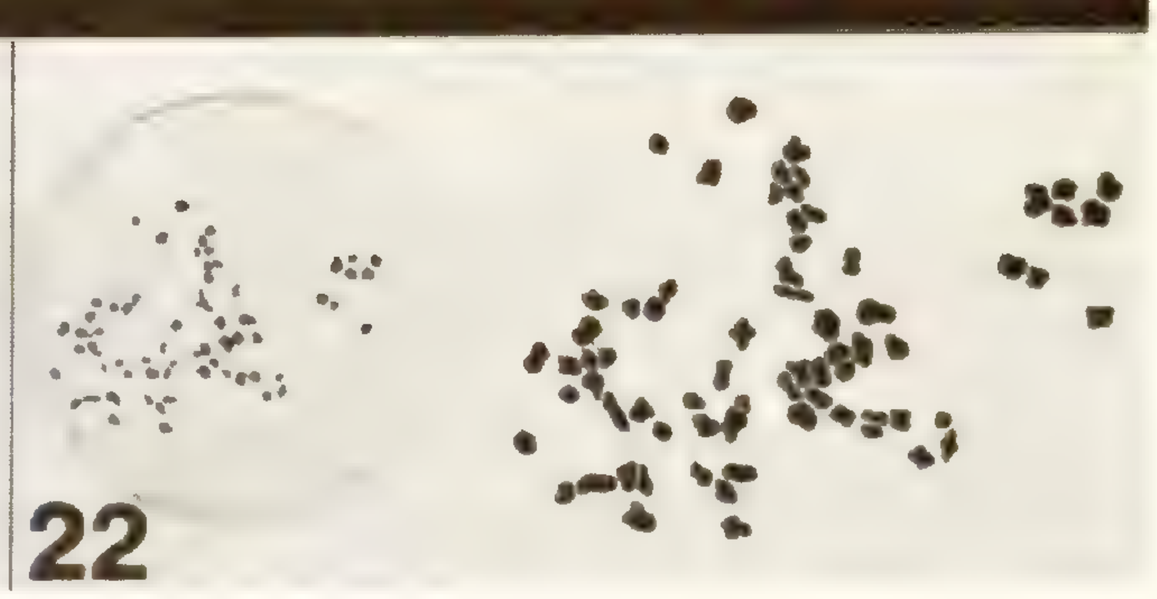
Peduncle and strobilus.—A single strobilus forms atop each slender, unbranched peduncle (*Figs. 1, 16* and *17*). In any one clone there are many sterile plants. The fertile plants usually produce only a single peduncle, which arises anisodichotomously from the dorsal side of the rhizome.

The peduncle and its reduced leaves remain green until the strobilus has fully differentiated. Internally, the peduncle is compact, with a cortex divided into three distinct zones (*Fig. 18*). The stele is radially symmetrical with approximately eight xylem arms alternating with the phloem. One phloem mass was observed in the center of the stele surrounded by xylem. The inner cortex adjacent to the stele consists of a layer of thin-walled cells 3 or 4 cells thick. Around this is a layer of thick-walled sclerenchyma 4-6 cells wide, which is surrounded by an outer cortex of thin-walled cells 5-8 cells wide. A single-layered epidermis covers the peduncle. Mesarch leaf traces depart from the stele at a low angle and gradually diverge through the cortex. The protoxylem in the leaf traces of the peduncle is often destroyed, producing a lacuna.

The strobilus has six vertical ranks of sporophylls in alternating whorls of three. Like the peduncle, the strobilus lacks chlorophyll when mature. The sporophylls are tightly appressed and consist of an upright, externally exposed portion and a

hidden, stalk-like portion which connects the sporophyll to the strobilar axis. The stele is similar to that of the peduncle. There is a conspicuous inner cortex of thin-walled cells. The remainder of the cortex of the mature strobilus consists of a large mucilage canal (*Fig. 19*). This initially forms in the stalk-like portion of the sporophyll and extends into the strobilar cortex. Connections between similar





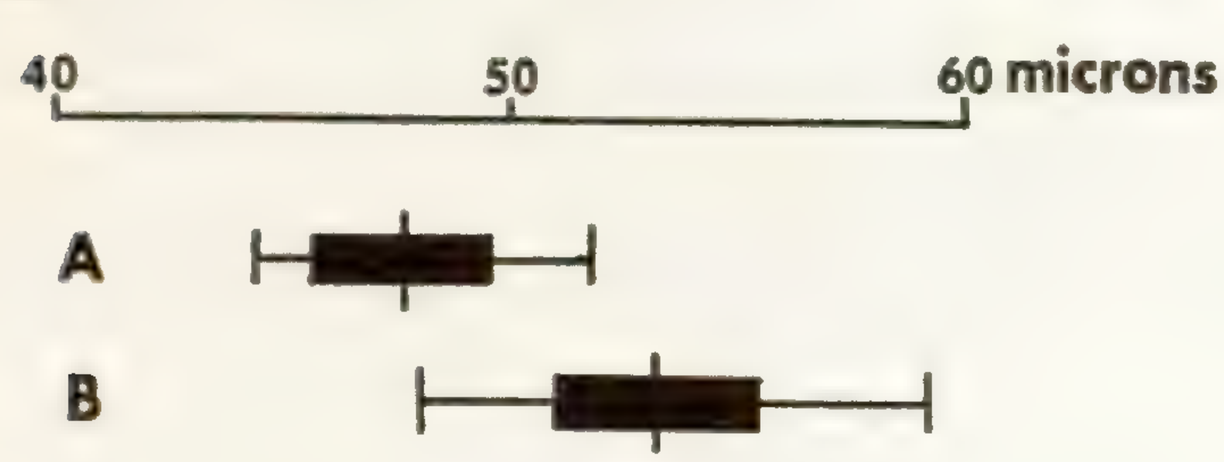
FIGS. 19-22. *Lycopodium carolinianum*. FIG. 19. Strobilus longisection with conspicuous, basal mucilage canals apparent as large clear spaces, × 12.5. FIG. 20. Young sporophyte with attached gametophyte (arrow), × 10.5. FIG. 21. Diploid chromosomes, $n=35$, interpretive drawing at right, first meiotic metaphase within spore mother cell wall at left. FIG. 22. Tetraploid chromosomes, $n=70$, interpretive drawing at right, first meiotic metaphase within spore mother cell wall at left.

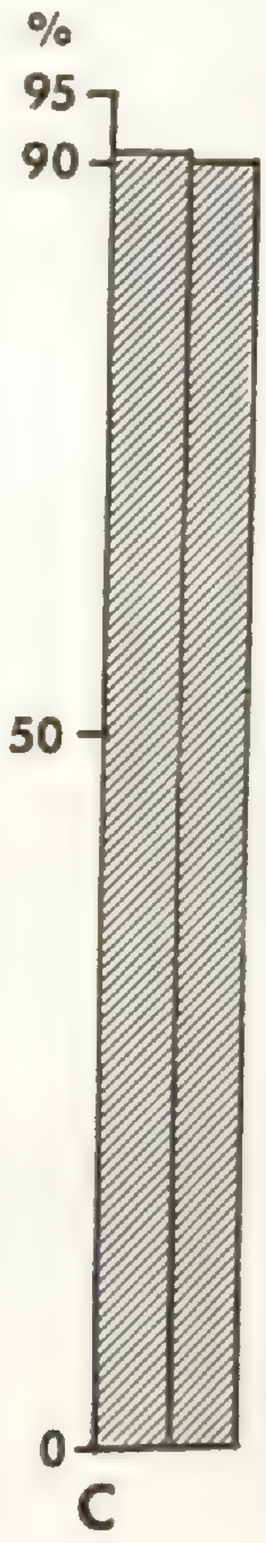
regions of adjacent sporophylls produce a mucilaginous cylinder within the strobilus. Development and maturation of these canals has been treated more fully in Bruce (1976). The mucilage cavity does not extend into the upright, exposed portion of the sporophyll.

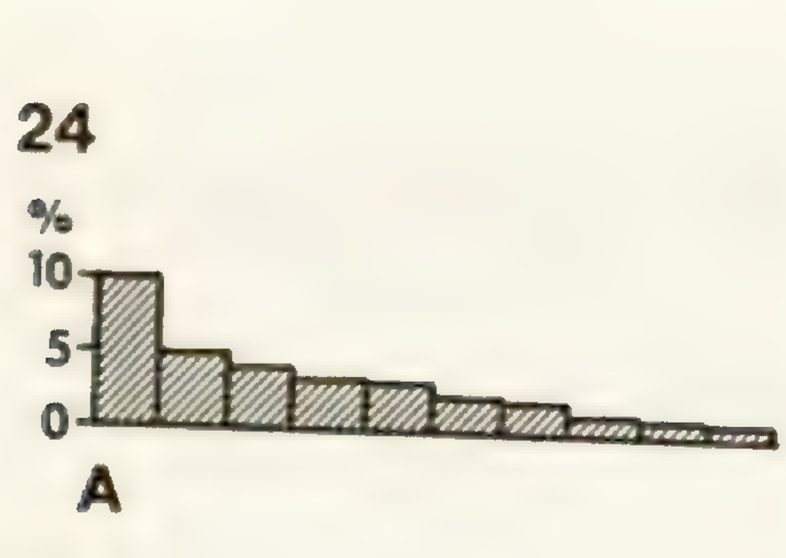
Chromosomes and spores.—Chromosomes were counted from one locality in North Carolina (Onslow Co., *Bruce 72028*) and another in Louisiana (Beauregard Pa., *Bruce 73147*). Several clear counts were obtained from each locality. In North Carolina, meiotic material had $n=35$ (*Fig. 21*). In Louisiana, a meiotic count of $n=70$ was obtained (*Fig. 22*). Plants from the two localities are morphologically identical, except for spore size. A count of 115 chromosomes,

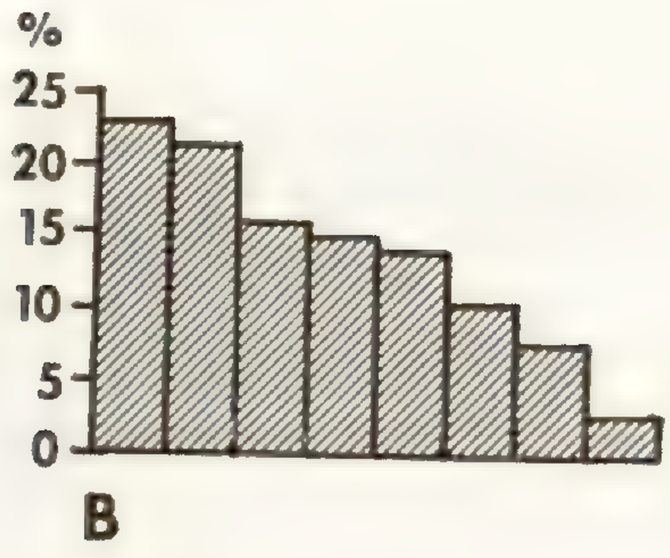
based on somatic material, was obtained from additional Louisiana material in which considerable spore abortion had occurred. The chromosomes vary in size, with several somewhat larger than the others.

Spore size is bimodal and correlates with the different chromosome numbers (*Fig. 23*); North Carolina material has a mean of 48 μm and Louisiana material a mean of 53 μm. In addition, spore abortion percentages were determined by counting the number of deformed spores in ten samples of 100 spores for each









FIGS. 23, 24. *Lycopodium carolinianum*. FIG. 23. Spore size distribution with range, mean, and one standard deviation on either side of the mean. FIG. 24. Spore abortion percentages based on 100-spore samples. A = diploid (10 samples), B = tetraploid (8 samples), and C = triploid (2 samples).

locality (*Fig. 24*). The North Carolina material is fairly uniform and generally has less than 10% abortion. However, the Louisiana material revealed two distinct groups: eight samples had less than 25% spore abortion, but two samples had ca. 90% spore abortion. The strobilus from which the somatic count of 115 chromosomes was taken also had many aborted spores in its more mature sporangia.

Gametophytes.—Sixteen gametophytes, eight with attached sporophytes, were found along a ditch in Onslow Co., North Carolina, during January, 1976. Some of the sporophytes were large enough to allow identification (*Fig. 20*). The gametophytes were green, surficial, and consisted of a tuberous body surmounted by numerous, photosynthetic lobes. All the gametophytes came from a small area near the ditch crest and all were associated with mature *L. carolinianum*.

DISCUSSION

Several features of *L. carolinianum* suggest a relationship with either subg. *Lepidotis* or subg. *Lycopodium*. These features are summarized in *Table 1* and are discussed below.

Lycopodium carolinianum occupies the same moist habitat as many members of subg. *Lepidotis* in the Gulf and Atlantic coastal plain. Ballard (1950) points out a similar habitat for African specimens of *L. carolinianum*.

The habit of the plant, with its repeatedly dichotomous but relatively short-lived rhizomes, is similar to that of *L. inundatum* L., *L. alopecuroides*, *L. prostratum* Harper, and *L. appressum* (Chapm.) Lloyd & Underw., all of subg. *Lepidotis*. Although the rhizomes in both subg. *Urostachys* and subg. *Lycopodium* also die off from behind, Primack (1973) has shown the rhizomes of these subgenera to be more long-lived.

The rhizome has a mixture of morphological and anatomical features of both subg. *Lepidotis* and subg. *Lycopodium*. The absence of veinal mucilage canals throughout the plant combined with the presence of basal mucilage canals in the strobilus is strongly suggestive of subg. *Lycopodium* (Bruce, 1976). This is also true of the related species *L. drummondii* Spring and *L. meridionale*. Chu (1974) found the rhizome leaves in *L. carolinianum* to correspond to the leaves of subg. *Lepidotis* in characters of the epidermis, mesophyll cells, and vascular bundles. Lastly, the presence of storage tubers formed from the stem tips suggests similarity to subg. *Lepidotis*. These perenniating tubers are closely comparable to structures found in *L. alopecuroides* and *L. prostratum*, both belonging to subg. *Lepidotis*.

Ballard (1950) stated that the tubers of African lycopodiums formed toward the end of the rainy season as a means of surviving an intense dry season. The situation in North American plants seems different. The tubers are formed infrequently and always toward the end of the warm season. There is no dry season to avoid. Freezing likewise is not limiting, for many plants which do not form tubers survive winter conditions. The low, wet areas in which these plants grow, however, contain much surface litter by late winter or early spring as a result of the death of the above ground parts of grass and other plants. Thus, frequent grass fires may occur, and tuber formation in North American *L. carolinianum* may be an adaptation allowing the plants to withstand these fires.

The few papers dealing with the roots of *Lycopodium* are almost entirely restricted to histological descriptions of root origin and development (Bruchmann, 1874, 1898; Pixley, 1968; Saxelby, 1908; Stokey, 1907; Van Tiegham & Douliot, 1888). In general the roots are relatively simple in structure, with a single xylem strand that is C-shaped in cross-section in the center. The horns of the C are pointed away from the stem stele. However, in certain species the roots at their origin from the parent stele are almost indistinguishable from it (Pixley, 1968, illustrates two of these). The ultimate rootlets of these species are typical of other roots of *Lycopodium*, with their characteristic C-shaped pattern. In subgenera *Lepidotis* and *Urostachys*, the root steles are always simple C-shaped structures. However, in at least ten species of subg. *Lycopodium* (*L. alpinum* L., *L. an-*

notinum L., *L. clavatum*, *L. complanatum*, *L. deuterodensum* Herter, *L. flabelliforme* (Fern.) Blanch., *L. obscurum* L., *L. sitchense* Rupr., *L. tristachyum* Pursh, and *L. volubile* Forst.) they are the elaborate, polyarch type when they first depart from the stem stele. Furthermore, the roots of subg. *Urostachys* descend through the cortex for long distances before emerging from the plant. Thus, *L. carolinianum* with its directly emergent roots and simple, C-shaped strand pattern corresponds to the root type found in subg. *Lepidotis*.

Nägeli and Leitgeb (1868) found that the root hairs of *L. clavatum* originate by an oblique division of the young cells in the protoderm. This forms a wedge-shaped cell from the proximal portion of the protodermal cell. Further divisions in the root hair initial, which was so formed, leads to the formation of multiple hairs. The same situation was found by Leavitt (1904) in *L. annotinum*, *L. dendroideum* Klotzsch, *L. lucidulum* Michx., *L. obscurum*, *L. sabinifolium* Willd., and *L. sitchense*. Stokey (1907) found the same in *L. pithyoides* Schlecht. & Cham. However, Leavitt (1904) determined that in *L. inundatum* a straight rather than an oblique wall forms in the protodermal cell. This division splits the protodermal cell into two nearly equal components, the distal one forming the elongate epidermal cell and the proximal one elongating perpendicular to the axis to form the root hair. The condition found in *L. carolinianum* is similar to that in *L. inundatum*. This is further evidence of relationship of *L. carolinianum* to subg. *Lepidotis*.

An endodermis was not recognized. However, the conspicuous cortical lacuna apparently functions as a physical barrier to the movement of water and ions from the root stele through the cortex to the exterior of the plant. Whether this applies also to the roots of other species is unclear. Stokey (1907) states that an endodermis consisting of cells with suberized walls exists in *L. pithyoides*. Russow (1872, p. 130) observed that in *L. inundatum* and *L. selago* L. the endodermis of the root is only a single cell in thickness. Roberts and Herty (1934), in a study of the anatomy of *L. flabelliforme*, concluded that an endodermis is not readily identified. They based their conclusion on chemical tests for lignin, cutin, and other common wall constituents as well as on anatomical studies. The endodermis in *Lycopodium* needs further study.

The peduncle is a thin, sclerenchymatous organ which resembles those found in subg. *Lycopodium*. Similarly, the strobilus with its reduced, modified sporophylls is most closely paralleled in sugb. *Lycopodium*. As discussed earlier, the mucilage canal distribution in the strobilus is indicative of subg. *Lycopodium*. Øllgaard (1975) has shown, however, that the thickening of the walls in the external cells of the sporangium of *L. carolinianum* is of a type restricted to subg. *Lepidotis*.

Chromosome numbers in *Lycopodium* correlate well with morphological features in defining taxonomic groups. In general, subg. *Lepidotis* has $n=78$ and subg. *Lycopodium* $n=23$ or 34. Löve and Löve (1958) observed $n=39$ in *L. carolinianum*. This corresponds with subg. *Lepidotis*, which has exactly twice this number. However, meiotic material proved to have $n=35$. A possible explanation of this discrepancy is size variation in the chromosomes. Large chromosomes might have been interpreted as being two small chromosomes. Cytological difficulties in *Lycopodium* have been recognized for many years (Manton, 1950, p.

246). Wilce (1965) points out specifically difficulties due to size variation. I also believe this is one of the chief problems.

The count of $n=35$ in *L. carolinianum* is phenetically closer to $n=34$, the number characteristic of the *L. clavatum* group of subg. *Lycopodium*, than to $n=78$, the number characteristic of subg. *Lepidotis*.

The chromosome numbers and spore size and abortion data support an hypothesis of autotetraploidy with subsequent back-crossing to produce a sterile triploid. Plants with a chromosome number of $n=35$ and normal spores are diploids; those with of $n=70$ and larger spores, but morphologically indistinguishable otherwise, are tetraploids; those with $n=115$ and aborted spores are triploid hybrids.

TABLE 1. CHARACTER COMPARISON BETWEEN *Lycopodium carolinianum* AND SUBGENERA *Lepidotis* AND *Lycopodium*.

Character	*subg. Lepidotis*	*L. carolinianum*	*subg. Lycopodium*
Habitat	moist	moist	dry
Habit	"annual"	"annual"	3, 4, or 5 years
Leaf epidermal cell wall	straight	straight	undulate
Veinal mucilage canal	present	absent	absent
Rhizome tuber	present or absent	present or absent	absent
Root stele pattern	C-shaped	C-shaped	polyarch initially
Root hair origin	straight division?	straight division	oblique division
Peduncle leaves	like rhizome leaves	reduced, modified	reduced, modified
Sporophylls	like rhizome leaves	reduced, modified	reduced, modified
Sporangium cell walls	straight, thin and unlignified	straight, thin, and unlignified	sinuate, thin, and lignified
Spore surface	rugulate	rugulate	reticulate
Chromosome number (n)	78	35	23, 34
Gametophyte habit	surficial	surficial	subterranean
Gametophyte nutrition	hemisaprophytic	hemisaprophytic	holosaprophytic

Wilce (1972) has shown that external spore morphology closely resembles that of the *Lepidotis* group.

Koster (1941) previously reported the gametophytes of *L. carolinianum* as green and surficial. Unfortunately, he neither illustrated nor described them. They appear, based on the present collection, similar to those described for subg. *Lepidotis* (Holloway, 1916, 1920; Treub, 1884, 1888; Goebel, 1887; Chamberlain, 1917). Gametophytes of the other two subgenera are either subterranean or epiphytic.

Lycopodium carolinianum provides a mixture of features combining characteristics of subg. *Lepidotis* and subg. *Lycopodium* (*Table 1*). The majority of characters demonstrate a closer phenetic similarity to subg. *Lepidotis*. While *L. carolinianum* appears properly placed in subg. *Lepidotis*, its peduncle and strobilar morphology, mucilage canal arrangement, and chromosome number suggest that a new section be erected to accommodate it.

Previously, Pritzel (1900) included *L. carolinianum* in sect. *Inundata*. He divided the section into two groups, one including *L. carolinianum*, the other *L. inundatum*. The section held together primarily on habital features. The other two

sections in the subgenus, *Lateralia* and *Cernua*, are both distinct on other grounds.

Lycopodium sect. Caroliniana Bruce, sect. nov.

A sectione Inundata foliis vegetativi canalibus mucosis destitutis, pedunculo gracili et strobilo compacto ut in subgenere Lycopodio, et chromosomatum numero $x=35$ differt.

TYPE SPECIES: *Lycopodium carolinianum* L.

Other species which may prove to be included in this section are *L. drummondii*, *L. meridionale*, *L. tuberosum* A. Br. & Welw. ex Kuhn, *L. paradoxum* Mart., *L. sarcocaulon* A. Br. & Welw. ex Kuhn, and *L. carnosum* A. Silv.

On the basis of the correlated trends of mucilage canal distribution and sporophyll specialization, Bruce (1976) argued that subg. *Lycopodium* was derived from elements within subg. *Lepidotis*. The features of *L. carolinianum*, i.e., its slender peduncle and compact strobilus, its mucilage canal arrangement, and its low chromosome number, which make it somewhat anomalous in subg. *Lepidotis*, are the general condition in subg. *Lycopodium*. This suggests that *L. carolinianum* arose from along the phylogenetic line which led from subg. *Lepidotis* to subg. *Lycopodium*.

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SHORTER NOTES

A RECORD OF OPHIOGLOSSUM VULGATUM L. FOR NORTH DAKOTA.—*Ophioglossum vulgatum* L. was collected in Richland County on July 21, 1974, 3.5 miles east and 1 mile south of McLeod (*Barker 6112*, NDA). A colony of 200-300 plants was found growing in a wet prairie meadow which is dominated by *Carex lanuginosa*. In observing the vegetation, it was possible to see the outline of a formerly cultivated field. The ferns were growing along the margin of this field, which had been abandoned for at least 30 years. This species is reported for St. Louis County, Minnesota and Cherry County, Nebraska. It is interesting to note that the plant occurs in a prairie meadow in the "Nebraska sandhills" and that the site in North Dakota also is in sandhills. This record represents a disjunct population of *O. vulgatum*, which is more common in the eastern U.S.—*William T. Barker* and *Jon Hanson, Department of Botany, North Dakota State University, Fargo, ND 58102.*

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Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of Drs. J. M. Baskin, A. M. Evans, R. H. Eyde, R. E. Holttum, R. M. King, J. H. Kirkbride, Jr., R. M. Lloyd, H. E. Robinson, W. A. Shropshire, Jr., and J. J. Wurdack. We welcome suggestions of other reviewers and offers of assistance.–D.B.L.

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ERRATA

P. 13, line 37. For "Loxsomacae" read "Loxsomaceae."

P. 39, line 10. For "northwest" read "northeast."

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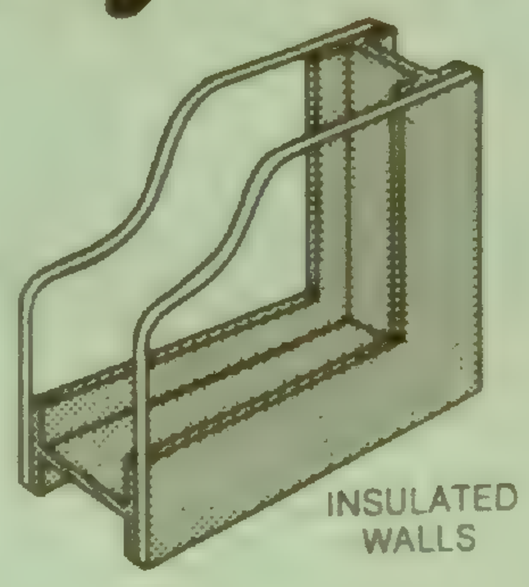

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Substrate Penetration by the Corm of Isoëtes

ERIC E. KARRFALT*

Several authors (Scott & Hill, 1900; West & Takeda, 1915; Osborn, 1922; Duthie, 1929) mention that the corms of various species of *Isoëtes* grow beneath the soil surface. Osborn gave the depth at which he found the corms of the adult plants as about two cm; some of the specimens of *I. nuttallii* supplied to me by Miss Vesta Hesse apparently grew at about the same depth, as indicated by the extent of the non-green, proximal portions of the sporophylls. Duthie reported finding corms at depths as great as 5-6 cm. Osborn and Duthie both worked with terrestrial species; I have found no references in the literature indicating the depth at which the corms of any aquatic species occur. However, the corms of aquatic species of *Isoëtes* (mainly *I. tuckermanii*) that I collected from several localities in New Jersey, Connecticut, and Massachusetts generally were buried so that the upper surface of the corm was about level with the surface of the substrate. Where the plants grew on fairly coarse gravel, their corms were only partly buried.

Observations on spore dispersal and gametophyte growth indicate that the gametophytes of some and probably all *Isoëtes* species live on or near the surface of the substrate, but no suggestions appear in the literature as to how the sporophytes become buried. In some cases sedimentation is apparently partly responsible for the corms becoming buried in the substrate, but this did not appear to be significant around the plants at most of the localities where I collected them.

In October 1971 and in September 1972 detached sporophylls of the aquatic *I. tuckermanii* were seen floating on Ames Long Pond in eastern Massachusetts. The same has been observed with sporophylls of *I. bolanderi* (Robert Dennis, pers. comm.). It is likely that water movement regularly detaches the bouyant, air filled sporophylls of the aquatic species as they begin to decay at the end of the growing season. As the sporophylls decay further, the sporangia and/or individual spores sink to the bottom, where presumably the gametophytes and sporelings develop. *Isoëtes tuckermanii* sporelings in Ames Long Pond do indeed develop at or near the surface of the substrate, although their exact position was difficult to determine because of the extremely loose nature of the highly organic muck in which the plants were growing.

In at least one terrestrial species (*I. drummondii*), spores are deposited on the soil surface (Osborn, 1922), and therefore it is possible that the gametophytes and sporelings also develop on the surface. Duthie (1929) reports that the spores of terrestrial species are dispersed in the soil by earthworms. Even if the germination of spores originally deposited upon the surface were delayed until they had somehow become passively buried, it seems unlikely that the sporelings of any species could survive at the depths at which adult corms are found, for the limited food reserves of *Isoëtes* megagametophytes requires that the sporelings become nutritionally self-sufficient at an early age. The first few leaves of the sporeling are very

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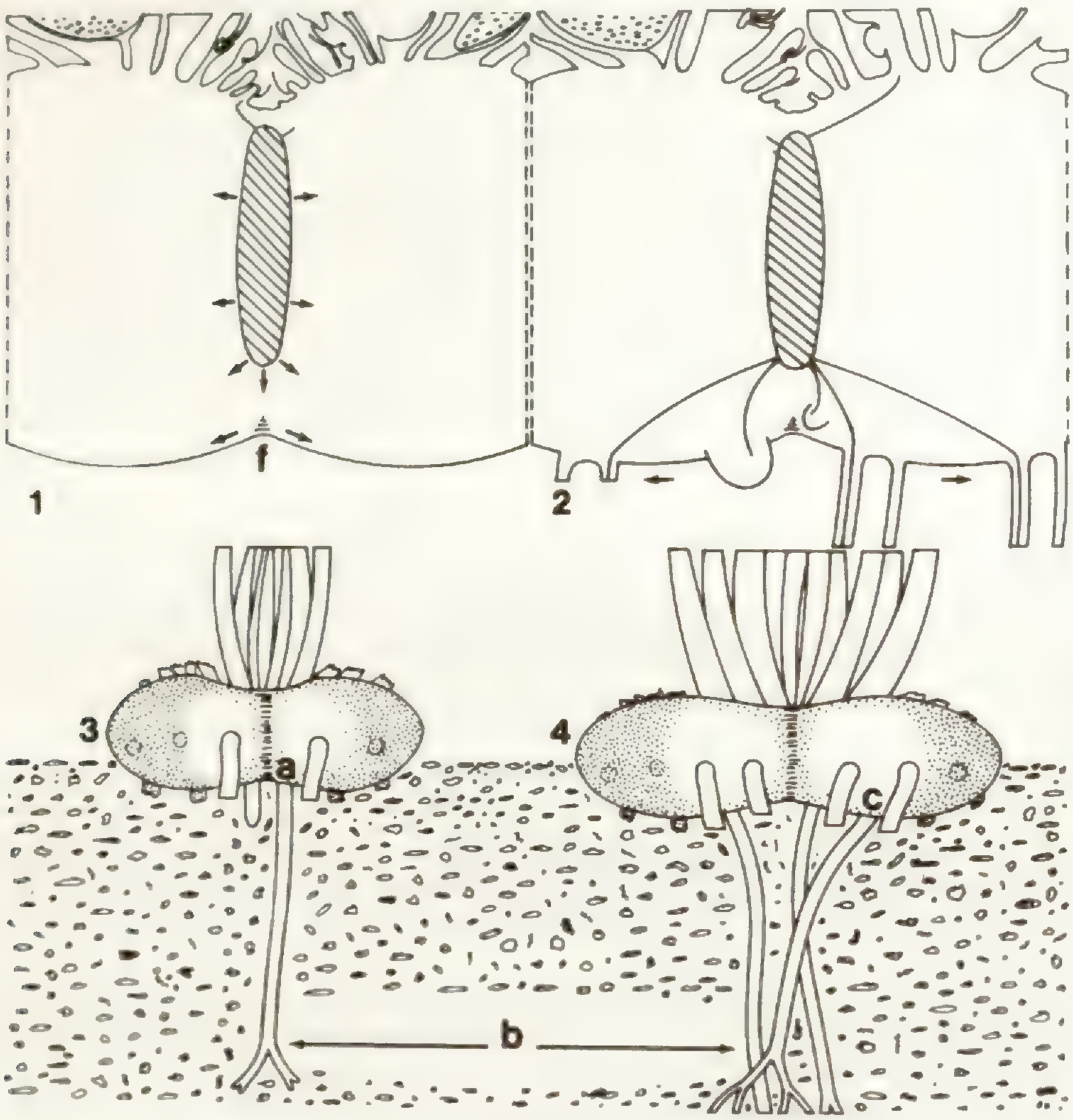
slender and not more than about one centimeter long, and by the time these are produced the megagametophyte has been reduced to a layer of empty cells stretched about the globose, embryonic foot. If the megagametophyte were buried more than a few millimeters, it would seem that the sporelings would exhaust their food reserves before their leaves could reach the light.



FIGS. 1-2. Diagrammatic longitudinal sections at right angles to the furrow of a two-lobed corm of *Isoëtes*. FIG. 1. Section between root orthostichies, × 16. FIG. 2. Section through a root orthostichy, × 16. f = furrow; arrows = direction of cortical tissue displacement; hatching = stele. FIGS. 3-4. Diagrammatic exterior views of a young, two-lobed corm of *Isoëtes*. FIG. 3. Early in a growing season, × 8. FIG. 4. Later in a growing season, × 8.

The mechanism by which *Isoëtes* corms become buried evidently is a mechanical consequence of their peculiar manner of root production. The main features of this mechanism are illustrated in *Figs. 1-4* using the example of a two-lobed form in which the sides and bottom of the corm are divided by a single furrow. *Figure 1* is a diagrammatic representation of a longitudinal section cut between root orthostichies at right angles to the furrow (*f*). The stele is represented by the hatched area at the center; it is completely surrounded except at its upper end by a continuous layer of meristematic cells (the basal and lateral meristems) which adds some vascular elements and parenchyma to the stele but which principally

cuts off additional cortical cells to the exterior, as indicated by the arrows directed away from the stele. The furrow is maintained at a constant distance from the stele by the destruction of cells at the bottom of the furrow at a rate which balances that at which new cells are added to the cortex at the base of the stele. As a result of this relationship, the cortical tissue on either side of the furrow is constantly being displaced from the furrow, as indicated by the lowermost pair of arrows. The cells which are destroyed at the bottom of the furrow actively elongate prior to being ruptured by the elongation of similar cells deeper within the corm (Karrfalt, in prep.).

Figure 2 also represents a longitudinal section cut at right angles to the furrow, but one which includes a root orthostichy on each lobe of the cortex. Each root orthostichy begins at a point on the basal meristem at which a root primordium arises and includes a row of roots which can be connected by a line drawn at a high angle to the basal meristem (about 90° in two-lobed plants; about 60° in three-lobed plants). The lowermost portion of the stele expands laterally in the plane of the furrow and bears a number of other sites of root initiation along its lower edge that produce additional orthostichies of roots parallel to the one in the plane of section shown in *Fig. 2*. The root primordia arise near the lower edge of the stele and develop within the cortex as they are displaced from the stele by continued meristematic activity about the stele. By the time a primordium reaches the level of the furrow, the root apex is fully formed. The root then grows out of the cortex just at the edge of the furrow and penetrates the substrate. Subsequent splitting of the cortical tissue at the furrow continues to expose additional tissue on either side of the furrow. The roots which are attached at various points on the surface of the cortex are thus displaced laterally from the furrow, as indicated by the arrows.

The effect of root production and growth on the position of the roots with respect to the substrate is illustrated in *Figs. 3* and *4*. *Figure 3* represents a young plant early in the growing season after a few new leaves and roots have been produced. One indicator of the age of *Isoëtes* plants is the shape of the cortical lobes, which become more rounded and eventually quite flat as layers of cortex are shed each year (Karrfalt, in prep.). The heavily stippled, peripheral portions of the the corm in *Figs. 3* and *4* represent dead cortex which was produced in the previous growing season. The relationship between the roots of the lowermost orthostichy and the substrate will be used as an example of the relationship that exists between all the roots and the substrate; those on the side of the corm are truncated in the figures to allow a better view of the lowermost roots. In *Fig. 3*, a root has emerged from the cortex at point *a*, grown downward in the substrate, branched, and become more or less anchored in the substrate at level *b*. *Figure 4* represents the same plant after additional growth has occurred. The root which had emerged at point *a* has now been displaced from the edge of the furrow to point *c*. Two effects result from the displacement of the root from point *a* to point *c*: a certain amount of substrate material lodged between the roots is pushed out from under the corm and tension is created in the roots which tends to pull the corm downward. This tension is a simple mechanical consequence of the fact that point *c* is farther from point *b* than is point *a*. Moreover, the resistance of the

substrate material to lateral root displacement tends to distort the root from the shortest course between points *c* and *b*, further increasing tension within the root. These two effects operate simultaneously on all of the roots and are the only aspects of corm growth that can account for the corms' becoming buried as they develop. Clearly the root tension force is small and limited by the short distances roots are displaced and by the low tensile strength of the root tissues. But coupled with the tendency of the roots to excavate material from under the corm, the small forces exerted by individual roots collectively constitute a marvelously efficient mechanism which has no exact counterpart among other living plants. Probably the nearest analog of the action of *Isoëtes* roots is that of the contractile roots of bulb-forming monocots. Although contractile roots are quite effective in pulling the bulbs down in the soil, there is no accompanying means by which material is removed from beneath them, and the soil eventually becomes densely compacted under the bulbs, a relatively crude mechanism compared with that present in the "lower" vascular plant, *Isoëtes*.

Although the process of substrate penetration seen in *Isoëtes* is unique among living plants, essentially the same process may have operated in the lobed bases of the various fossil lycopods which are thought to be related to *Isoëtes*. If this were the case, it becomes much easier to understand how the columnar plant body of *Pleuromeia*, for example, was kept upright: the roots of these plants may not have functioned primarily as supportive structures, but may have served simply to bury the lower end of the axis, which then stood in the soil like a fence post.

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A New Species of Trichomanes from Eastern Africa

ROBERT B. FADEN*

Like many groups of tropical ferns, the family Hymenophyllaceae is not well represented in continental Africa, where only 30–35 species occur. Despite the moderate number, there is still some disagreement about the specific limits of several species (cf. Schelpe, 1970; Faden, 1974). There has not been a continent-wide study of the family since the generic monograph of Copeland (1938), which is incomplete in species coverage and lacks species descriptions. No new species has been described from mainland Africa since Alston (1956).

While I was working at the East African Herbarium from 1969 to 1972, I made several collections of a *Trichomanes* which appeared to represent an undescribed species. Herbarium studies at the Royal Botanic Gardens, Kew and British Museum (Natural History) confirmed this conclusion and revealed that the species is widespread in eastern Africa. Field investigations also showed that it is ecologically distinct from its relatives in East Africa.

Trichomanes ramitrichum Faden, sp. nov. **Figs. 1–5**

Trichomanes sp. *A*. of Faden *in* Agnew, Upland Kenya Wild Fls. 29. 1974.

Trichomanes borbonicum v. d. Bosch *sensu* Schelpe *in* Exell & Launert, Fl. Zambesiaca 76. 1970, *pro parte*.

Trichomanes pyxidiferum L. var. *melanotrichum* (Schlechtend.) Schelpe *sensu* Schelpe, *op. cit*. 78, *pro parte*.

Rhizoma filiforme modice dense vestitum trichomatibus brunneis aliquibusque monopodialiter ramosis. Frondes plerumque bi- vel tripinnatifidae, in ambitu ovatae ad lineares, 2–14 cm longae, 0.8–3 cm latae, in siccitate plicis, venis falsis carentes. Indusium tubulare, 2–2.5 mm longum, apice bilabiatum, labiis plerumque haud expansis.

TYPE: KENYA, Kericho District, South West Mau Forest, along the Kiptiget (Chepkoisi) River, ca. 16 km SSE of Kericho, 0°31′–0°31′30″S, 35°18′–35°19′30″E, 1980–2020 m, 12 June 1972, *Faden & Grumbley 72/338* (EA; isotypes B, BM, BOL, BR, DSM, GH, K, LISC, LMU, MHU, MO, P, PRE, SRGH, US, WAG, Herb. Pichi-Sermolli).

Rhizome filiform, moderately densely and usually persistently covered with dark brown trichomes, at least some trichomes monopodially branched; fronds remote, flabellately divided or, more commonly, 2–3-pinnatifid, ovate to linear in outline, 2–14 cm long, 0.8–3 cm wide; stipe 0.2–2.5 cm long, dark green, blackish at the base, winged in the upper part, with scattered, minute, clavate hairs on both surfaces and occasionally some longer hairs at the base; lamina glabrous except for sparse minute clavate hairs on the veins of both surfaces, false veins wanting, longitudinal drying folds present, pinnule lobes linear; indusia terminal on the basal acroscopic pinnule lobes and sometimes also on the terminal lobes of the pinnae and subterminal basiscopic pinnule lobes, tubular, 2–2.5 mm long, winged for 2/3–3/4 of their length, bilabiate above this, labia rounded to truncate at the apex, usually not spreading, entire or rarely denticulate at the apex, receptacle usually long-exserted.

DISTRIBUTION: Uganda, Kenya, Tanzania, Zambia, Rhodesia, and Mozambique.

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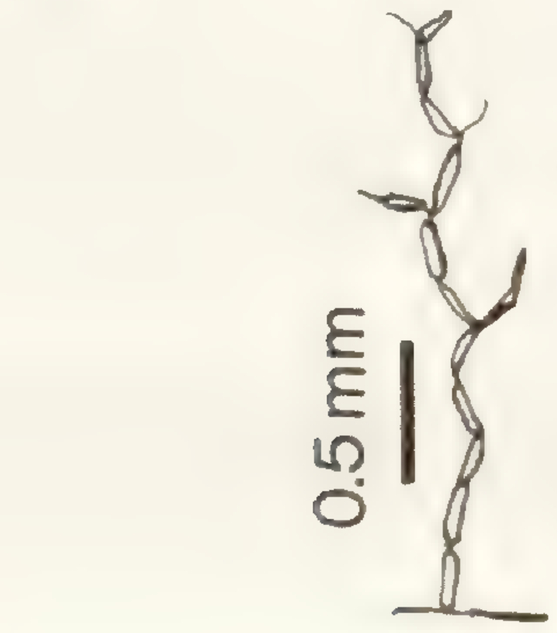

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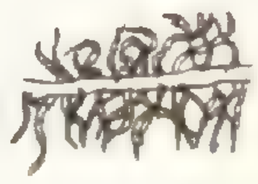

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FIGS. 1-5. *Trichomanes ramitrichum, Faden & Grumbley 72/338.* FIG. 1. Frond. FIGS. 2-3. Indusia. FIG. 4. Portion of rhizome with trichomes. FIG. 5. Branched trichome. FIGS. 6-7. *Trichomanes melanotrichum.* FIG. 6. Indusium, *Faden & Grumbley 72/337.* FIG. 7. Portion of rhizome with trichomes, *Faden et al. 71/893.* FIGS. 8-9. *Trichomanes borbonicum.* FIG. 8. Indusium, *Faden et al. 71/173.* FIG. 9. Portion of rhizome with trichomes, *Faden et al. 71/81.*

ADDITIONAL SPECIMENS EXAMINED:

UGANDA: Kigezi Distr.: Ishasha Gorge, 1400-1500 m, *Faden, Evans & Lye 69/1194* (EA, Herb. Pichi-Sermolli).

KENYA: Kakamega (North Kavirondo) Distr.: Malava (Kabras) Forest, 1620 m, *Faden & Evans 69/2045A* (BOL, EA, K, US, Herb. Pichi-Sermolli). **Kericho Distr.:** Near Tea Research Institute, 2080-2140 m, *Faden & Cameron 72/315* (EA, K, Herb. Pichi-Sermolli); Marinyn (Marnyn) Tea Estate, 1980 m, *Faden & Cameron 72/325* (EA, K, Herb. Pichi-Sermolli). **Taita Distr.:** Mt. Kasigau, 1250-1645 m, *Faden, Evans & Rathbun 69/478* (EA), and 1250-1400 m, *Faden et al. 71/142*, (EA, K, Herb. Pichi-Sermolli); Taita Hills, Mwambirwa Forest Station, 1300 m, *Faden, Evans & Smeenk 70/524* (EA, K, US, Herb. Pichi-Sermolli).

TANZANIA: Tanga Distr.: Eastern Usambara Mountains, Derema, 790 m, *Faden & Faden 74/362* (EA, K, MO). **Morogoro Distr.:** Mindu Mountains W of Morogoro, 1150-1230 m, *Pócs 6152/U* (BOL, EA, Herb. Pichi-Sermolli); Kanga Mountains, 1000-1100 m, *Pócs 6137/U* (EA).

ZAMBIA: Mpika Distr.: Muchinga Escarpment, Mukowonshi Mountain, 1800-1850 m, *Pócs & Kornaś 6629/E* (EA).

RHODESIA: Melsetter Distr.: Chimanimani Mountains, 1520 m, *Mitchell 340* (BM), and 1650 m, *Mitchell 421* (BM, EA); Melsetter, 1520 m, *Chase 4989* (BM, MO). **Umtali Distr.:** Stapleford Forest Reserve, 1620 m, *Chase 4516* (BM), and 1680 m, *Chase 7428* (K); Vumba Mountains, *Chase 5383* (BM), and 1650 m, *Chase 5987* (BM); Middle Gallery Wood, 1680 m, *Chase 7043* (BM, K).

MOZAMBIQUE: Without locality or date, *Mendonça 1398* (BM). **Manica e Sofala (Beira) Prov.:** Gorongosa (Zambesia), *Carvalho 7* (K). **Niassa (Moçambique) Prov.:** Ribaue Mountain, 1070 m, *Schelpe & Leach 6940* (K) [mixture with *T. melanotrichum*].

MORPHOLOGICAL VARIATION

The fronds of *T. ramitrichum* vary greatly in dissection. Most often they closely resemble those of *T. melanotrichum* Schlechtend. and *T. borbonicum* v. d. Bosch. One extreme form of *T. ramitrichum* has more flabellately divided fronds than usual *(Faden, Evans & Smeenk 70/524)*, and thus approaches *T. chevalieri* Christ in this character. Another variant *(Faden & Grumbley 72/338)* has some very narrow and little divided fronds. This form does not resemble any other African species of *Trichomanes* in cutting. Because the extreme forms are connected to the more typical types by intermediates, there is no basis for further taxonomic division of *T. ramitrichum*.

Variation in *T. ramitrichum* indusia also has been noted. Nearly all specimens have entire indusium lobes. One collection has the indusium lobes denticulate at the apex *(Faden, Evans & Lye 69/1194)*. Some plants of the type collection have a number of indusia with obscure apical teeth, and thus form connecting links between *Faden, Evans & Lye 69/1194* and other collections. Indusia with spreading lobes resembling those of *T. melanotrichum*, rather than appressed lobes, are also known *(Chase 7043)*, although some indusia of this collection have the usual appressed lobes of *T. ramitrichum*, and the rhizome trichomes are typical of that species.

RELATIONSHIPS

If the multigeneric concepts for the Hymenophyllaceae of Copeland (1938, 1947) are used, then *T. ramitrichum* would be included in *Vandenboschia* Copel. If the classification of Morton (1968) is used, the plant would belong in *Trichomanes* subg. *Trichomanes* sect. *Lacosteopsis* Prantl. The other continental African species belonging to the same section (or segregate genus) are: *T. af-*

ricanum Christ, *T. borbonicum* v. d. Bosch, *T. chevalieri* Christ, *T. fallax* Christ, *T. melanotrichum* Schlechtend., *T. mettenii* C. Chr., and *T. radicans* Swartz. (Some or all of the continental African specimens determined as *T. giganteum* Bory belong to *T. radicans, fide* Pichi-Sermolli, *in litt.*). *Trichomanes ramitrichum* differs from all of them in having branched rhizome trichomes and in the form of the indusium. Typical plants are most similar to *T. melanotrichum* and *T. borbonicum*, differing from the former in their longer, paler rhizome trichomes and generally proportionally narrower indusia (Figs. 2–4 vs. 6 and 7) and from the latter in their proportionally broader indusia (Figs. 2 and 3 vs. 8) and presence of drying folds on the lamina.

An indusium of the type found in *T. ramitrichum* is characteristic of the segregate genus *Crepidomanes* Presl (Copeland, 1938, 1947) or *Trichomanes* subg. *Trichomanes* sect. *Crepidomanes* (Presl) Prantl (Morton, 1968). Particularly similar in indusium form is the Malaysian *T. bilabiatum* Nees & Blume (cf. Holttum, 1954, p. 100, fig. 36). That species, however, like all others in the section/genus *Crepidomanes*, has false veins and is not closely related to *T. ramitrichum*. Furthermore, not every species of the section/genus *Crepidomanes* has a bilabiate indusium: *T. clarenceanum* Ballard, the sole continental African species of the section/genus *Crepidomanes*, and *T. christii* Copel. have indusia with entire, dilated mouths.

ECOLOGY

Trichomanes ramitrichum occurs chiefly in moist, submontane evergreen forests, but occasionally extends up into the montane forest zone. It is recorded from 790–2100 m altitude. It is primarily a low epiphyte on tree trunks, but it is sometimes lithophytic. Whether it occurs in both situations in any one locality is unknown. I have found it most abundant in the South West Mau Forest in Kenya, a montane forest, where it grows at its highest recorded altitude. This suggests that *T. ramitrichum* may well occur at higher elevations than collections to date would indicate.

Since *T. ramitrichum* frequently occurs with *T. melanotrichum*—there are a number of mixed collections—it is interesting to examine the ecology of the latter species. Taton (1946), in comparing the tolerances of the 18 species of Hymenophyllaceae then recorded from the Belgian Congo (now Zaïre), found *T. melanotrichum* (cited as *T. pyxidiferum* L.) to have the greatest altitude range and substrate diversity of any species. He also found it to occur in the greatest variety of habitats. I have found the same to be true for this species in East Africa with regard to altitude (760–3050 m) and habitat diversity. In substrate choice, however, *T. melanotrichum* appears to be no more diverse than several other East African species of *Trichomanes*, including *T. chevalieri* and *T. ramitrichum*. It occurs as a low epiphyte on tree trunks in moister habitats, or, less often, as a lithophyte near streams.

The most outstanding feature of the ecology of *T. melanotrichum* is this species' greater ability to endure dry seasons than any other East African filmy fern. This, in combination with its tolerance of a great range of temperatures (as

judged by its altitudinal range), allows it to occur in habitats too harsh for other species of Hymenophyllaceae. This accounts not only for its very wide distribution but also for its frequent occurrence as the sole member of this family in many localities.

Trichomanes melanotrichum is sympatric with *T. ramitrichum* throughout the latter's range and extends well beyond it in all directions. In the area of overlap, *T. melanotrichum* is very common while *T. ramitrichum* is much more local. In localities where both species are present—in Kenya and Uganda there are no unequivocal cases of *T. melanotrichum* being absent from a *T. ramitrichum* locality—they frequently are observed growing on the same tree trunks or rocks. It is possible that competition occurs between them, at least for substrate space. There is no direct evidence, however, that competition is a factor limiting the distribution of *T. ramitrichum*. Experimental studies to test this hypothesis would be interesting.

In contrast to the above comparison, the ecological requirements of *T. ramitrichum* and *T. borbonicum* appear to be quite distinct. Although their altitude ranges overlap considerably, the two species are not known to occur together. In the Taita Hills and on Mt. Kasigau, in Kenya, both species occur at their lowest elevations in the country because of the lowered altitudes of the vegetation zones on these isolated mountains due to the Massenerheburg effect (cf. Richards, 1952, p. 347). Even there, however, the two are altitudinally separated by at least 200 m in the Taita Hills and by 100 m on Mt. Kasigau. These small differences may seem insignificant, but they are correlated with other floristic discontinuities. Competition between the two species would be unlikely to occur in any event, in view of the preference for lithophytic substrates by *T. borbonicum* and for epiphytic substrates by *T. ramitrichum*.

To complete this survey of the ecological relationships among these three species of *Trichomanes*, a brief look at the relationship between *T. melanotrichum* and *T. borbonicum* is required. The latter species grows from about 1400–2500 m in East Africa but is uncommon below 2000 m. It is primarily a species of moist montane forest and the bamboo zone. In the latter zone, *T. melanotrichum* is decidedly uncommon. Where the two species occur together, *T. borbonicum* is usually lithophytic and *T. melanotrichum* epiphytic. Thus competition for substrate space would appear to be minimal.

The above three species show different degrees of ecological isolation from one another. Similar studies of other African species may help to solve some remaining taxonomic problems in the family.

I wish to thank Drs. F. M. Jarrett, R. E. G. Pichi-Sermolli, and E. A. Schelpe, and the late C. V. Morton for determinations of specimens and useful comments, and Michael Campbell for preparing the illustrations.

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Spore Morphology of Anemia Subgenus Coptophyllum

STEVEN R. HILL*

Anemia Swartz is a genus of leptosporangiate ferns consisting of approximately 90 species. The genus inhabits tropical and semitropical latitudes in Africa, India, and the Americas, with two species reaching the United States. *Anemia* generally is divided into three subgenera: *Coptophyllum*, *Anemiorrhiza*, and *Anemia*. The present study deals with a scanning electron microscopic examination of spores of six species of subg. *Coptophyllum*, four of which are endemic to the Planalto region of south-central Brazil.

Subgenus *Coptophyllum* has been monographed by Mickel (1962), who noted spore morphology as viewed with a light microscope. Previous studies of *Anemia* spores also include the work of Erdtman (1957). The spores of *Anemia* are unique among ferns in their tetrahedral shape and surface pattern of conspicuous ridges separated by striae. Protuberances or ridge extensions occur where the ridges join the trilete scar. The present study was undertaken in an attempt to discover morphological details not visible in light microscopy that might be of taxonomic value.

While I was the field assistant to Dr. William R. Anderson on the 1973 New York Botanical Garden Expedition to the Planalto region of south-central Brazil, I collected spore samples of various *Anemia* species. All were air-dried. Spore samples of six species, 18 specimens altogether, belonging to subg. *Coptophyllum* were mounted on aluminum studs with double-adhesive tape and coated with a thin (200–400Å) layer of gold-palladium. The samples were then examined at 15 kv and photographed using the JEOL JSM-U3 Scanning Electron Microscope (SEM) of the Electron Microscopy Center, Texas A & M University. To best facilitate comparisons, proximal, distal, and ornamentation micrographs were included for all species examined. Measures and magnifications are based upon those indicated by the instrument. Although absolute accuracy in magnification is rare in the SEM, relative measures between the spores can be assumed to be correct. In the following listing, collections cited with an asterisk are illustrated in this paper. The specimens examined, all of which were from Brazil, are:

A. elegans (Gardn.) Presl.—**Goiás**: Alto do Paraíso, *Anderson, Hill, et al. 6670*; Serra dos Cristais, *Anderson, Hill, et al. 8186;* Serra Dourada, *Anderson, Hill, et al. 9982;* Serra dos Pireneus, *Anderson, Hill, et al. 10295.** **Matto Grosso:** Barra dos Garças, *Anderson, Hill, et al. 9823.*

A ferruginea H.B.K.—**Goiás:** Alto do Paraíso, *Anderson, Hill, et al. 6794;* Serra dos Pireneus, *Anderson, Hill, et al. 10344.* **Minas Gerais:** Serro do Espinhaço, *Anderson, Hill, et al. 8415, 8767.** **Matto Grosso:** Barra dos Garças, *Anderson, Hill, et al. 9904.*

A. glareosa Gardn.—**Goiás**: Alto do Paraíso, *Anderson, Hill, et al. 6655;* Serra Dourada, *Anderson, Hill, et al. 9983.**

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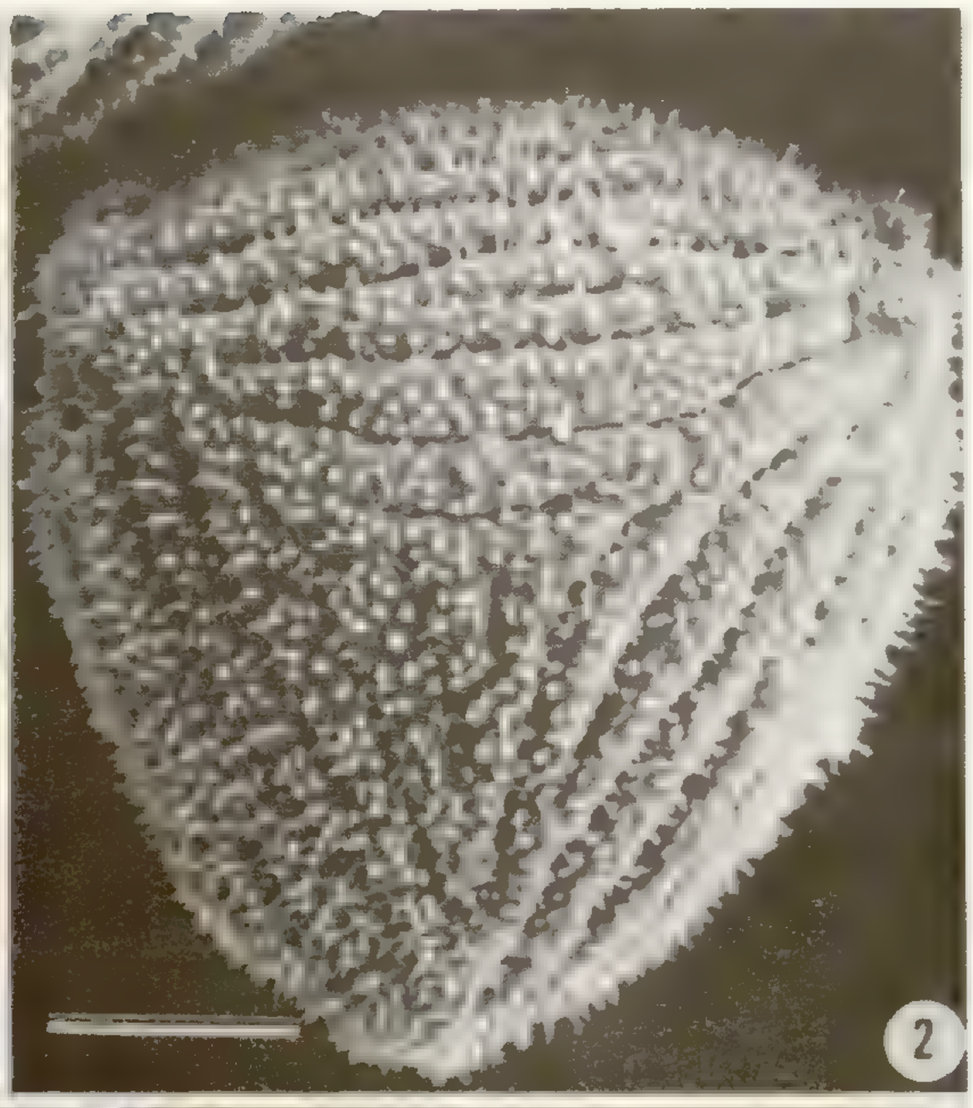
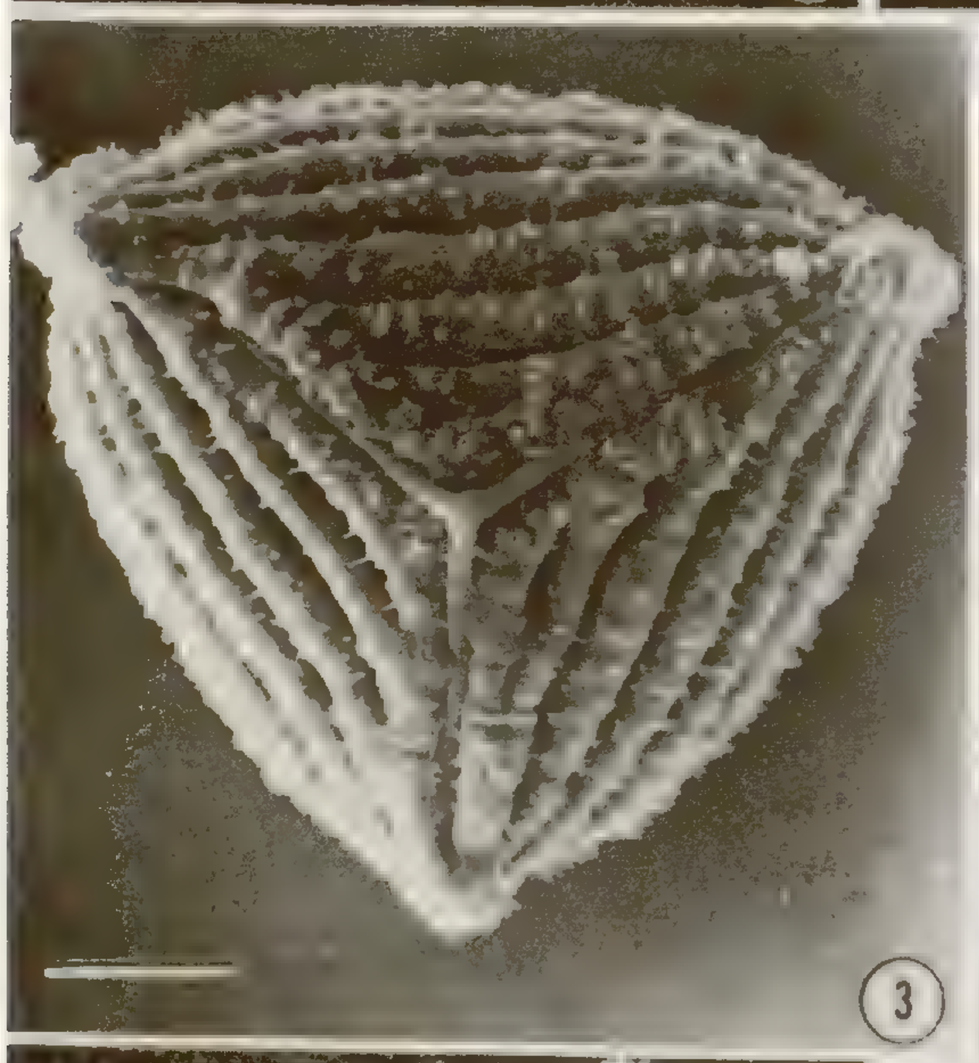
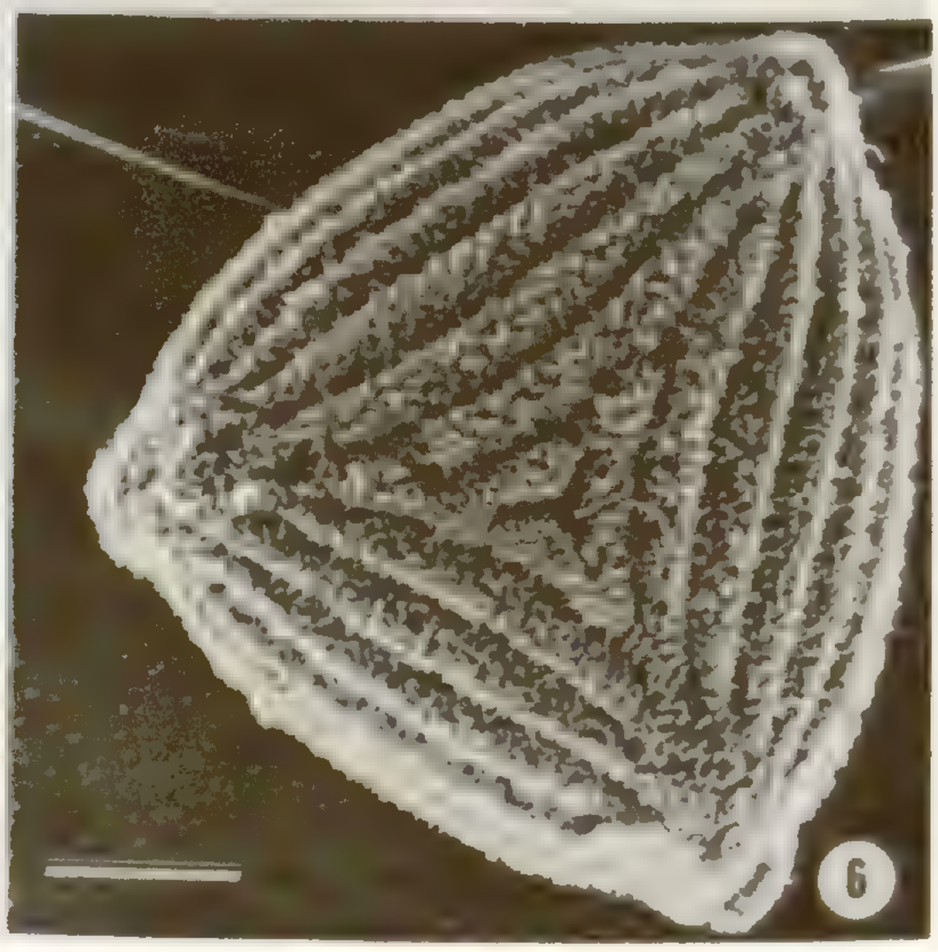
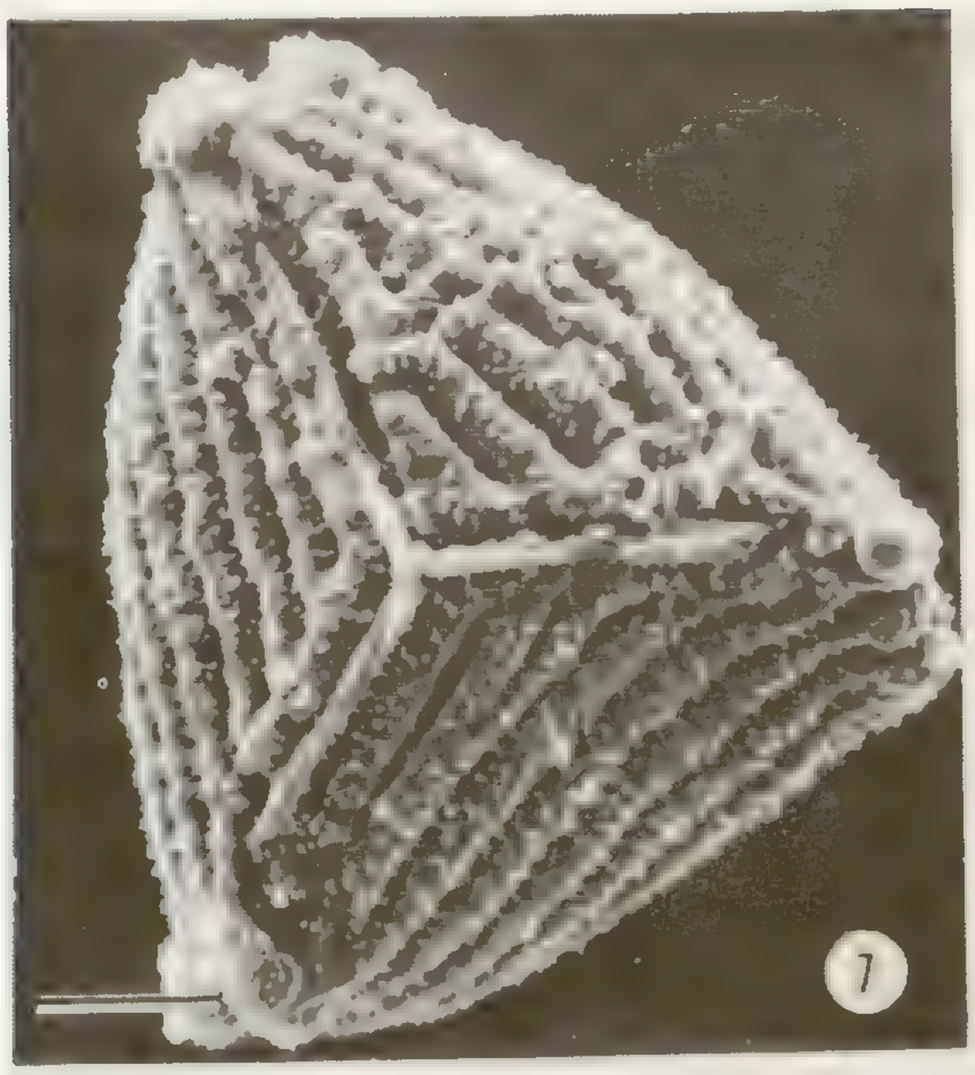
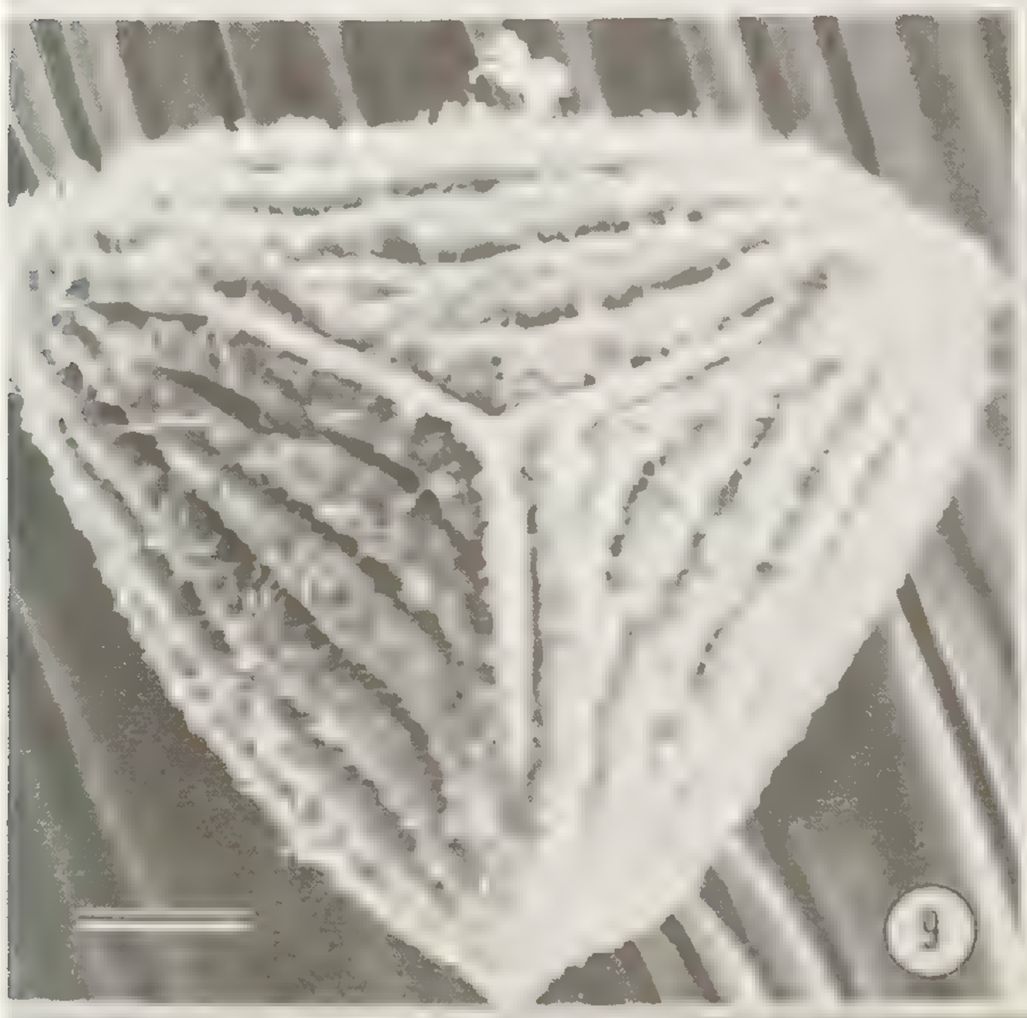


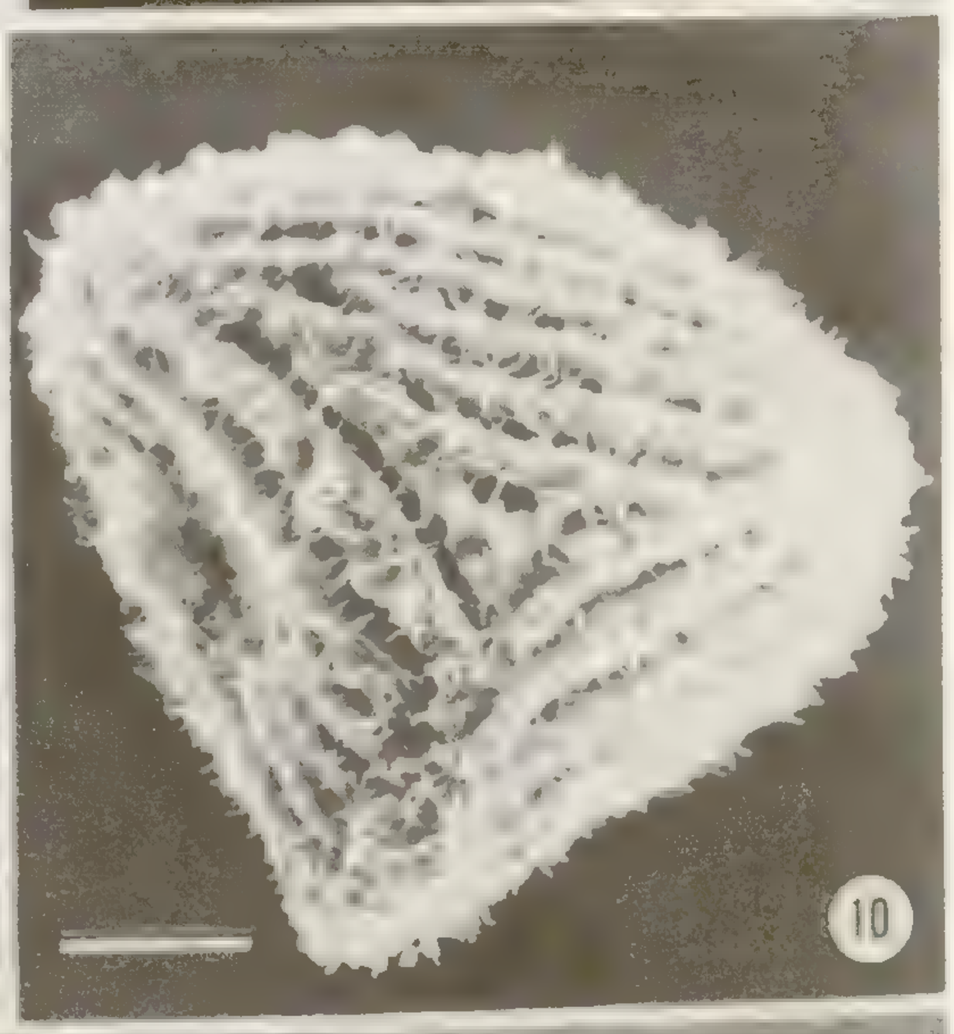


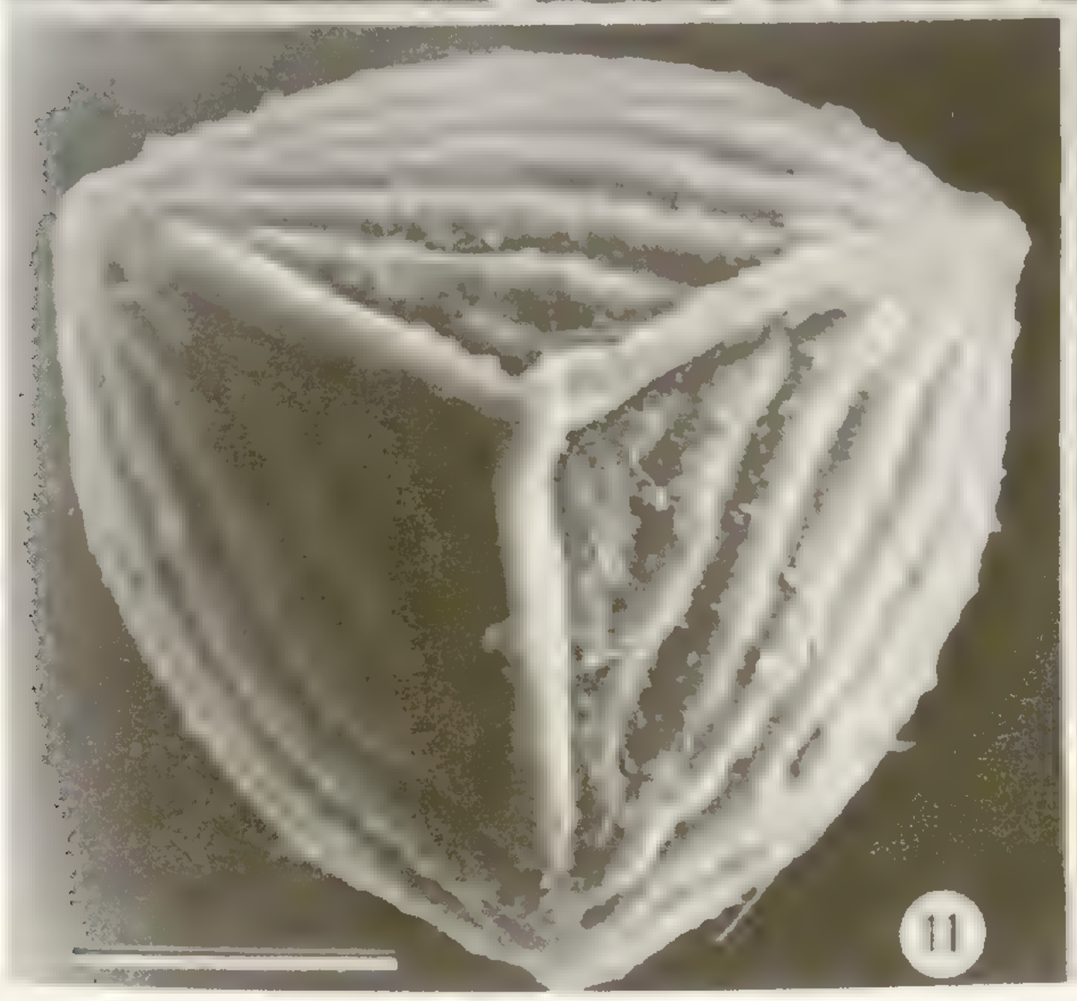


Proximal and distal views of *Anemia* spores; bar = 20 μm. FIGS. 1-2. *A. elegans*. FIGS. 3-4. *A. trichorrhiza*. FIGS. 5-6. *A. glareosa*.









Proximal and distal views of *Anemia* spores; bar = 20 μm. FIGS. 7-8. *A. ferruginea*. FIGS. 9-10. *A. tomentosa*. FIGS. 11-12. *A. rutifolia*.

A. rutifolia Mart.—**Minas Gerais:** Serra do Espinhaço, *Anderson, Hill, et al. 8418.**

A. tomentosa (Sav.) Swartz.—**Matto Grosso:** Barra dos Garças, *Anderson, Hill, et al. 9904.**

A. trichorrhiza Gardn. in Hook.—**Goiás**: Alto do Paraíso, *Anderson, Hill, et al. 6651;* Serra Dourada, *Anderson, Hill, et al. 9986;* Serra dos Pireneus, *Anderson, Hill, et al. 10300.** **Matto Grosso:** Barra dos Garças, *Anderson, Hill, et al. 9821.*

A set of voucher specimens was deposited in the herbarium of the Universidade de Brasília (UB) with all duplicate sets remaining at the New York Botanical Garden in preparation for distribution.

RESULTS

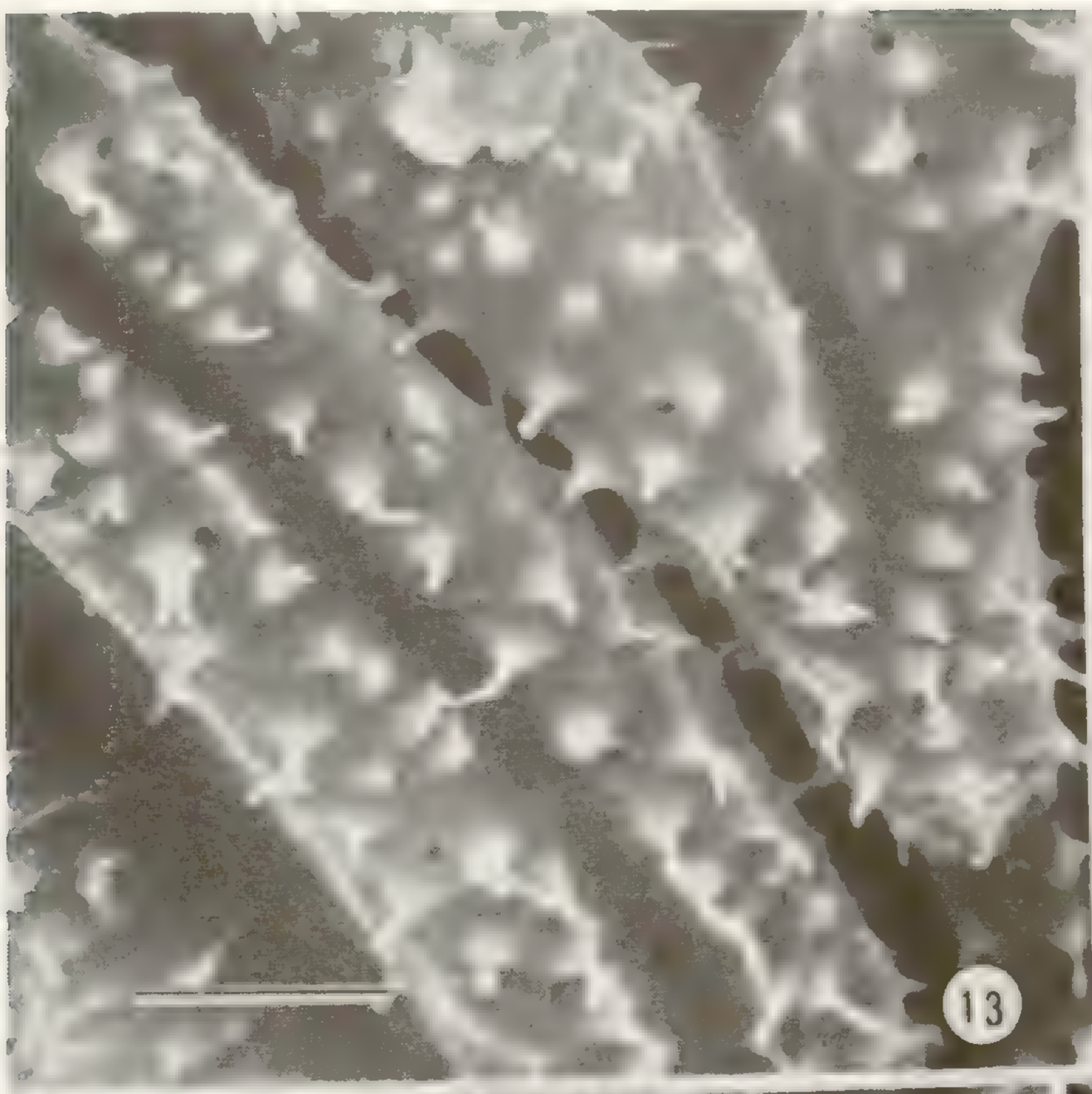
The primary variable encountered with respect to surface micromorphology of the *Anemia* spores is ridge ornamentation. In Mickel's (1962) treatment, the spore ridges of all six species studies are described as "smooth" or "clear," with the exception of *A. tomentosa*, whose spore ridges are described as "subverrucu-late." The present scanning electron micrographs demonstrate the limitations of the light microscope. In all cases but one (*A. rutifolia*), the spore ridges are seen to be scabrate (micro-echinate) or echinate; spine shape and size vary according to the species. In addition, micropores up to 0.5μm in diameter are visible on the ridges of most of the species studied.

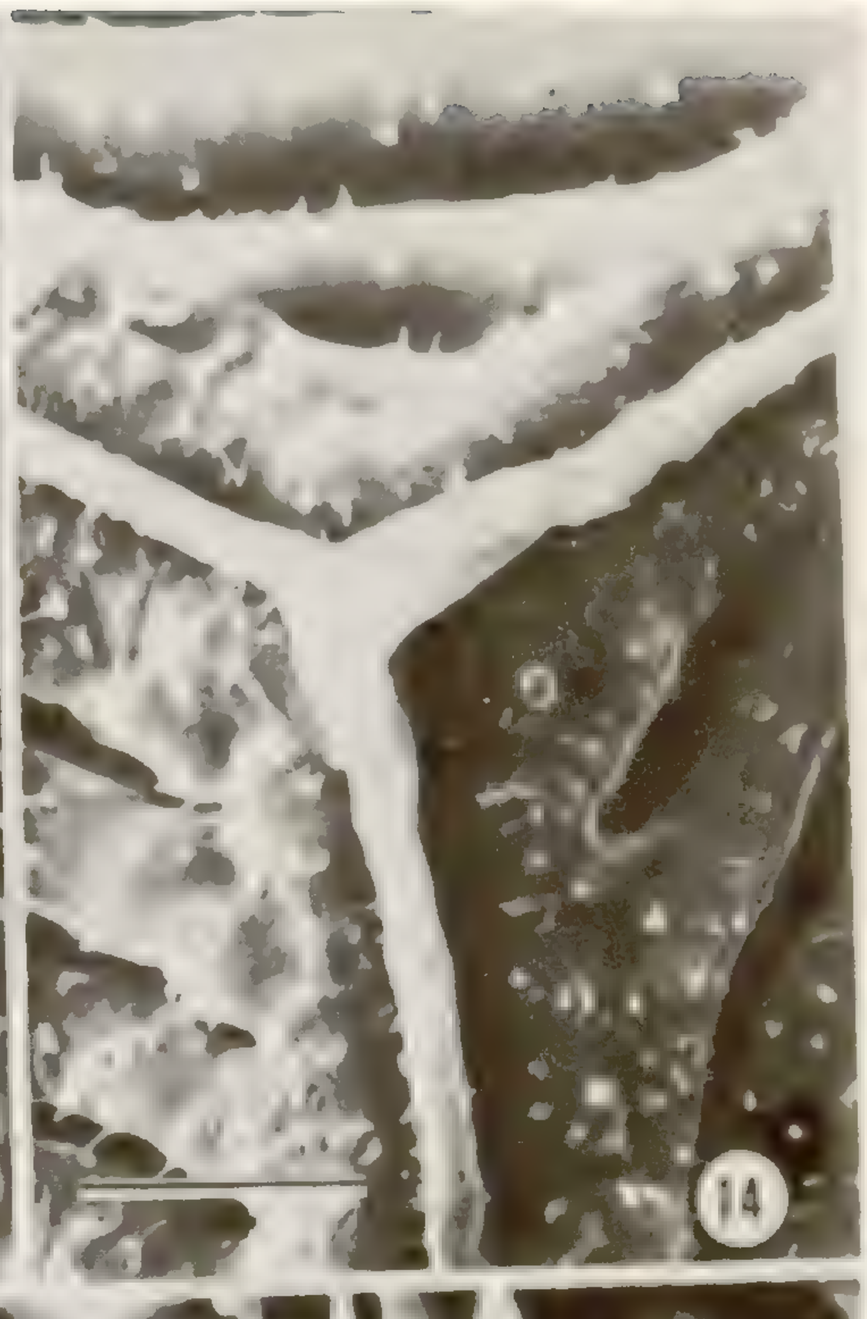
The spores of *A. elegans* (*Figs. 1, 2,* and *13*) have striking, wide ridges and angle protuberances. Echinate ornamentation is present on the ridges, and often bifurcate spines 1.0-1.4 μm long are present (*Fig. 13*). Several micropores are also visible on the ridge surface; their function possibly is that of air or water exchange or detection. The trilete scar also bears spines and gradually merges with the ridges at its extremities.

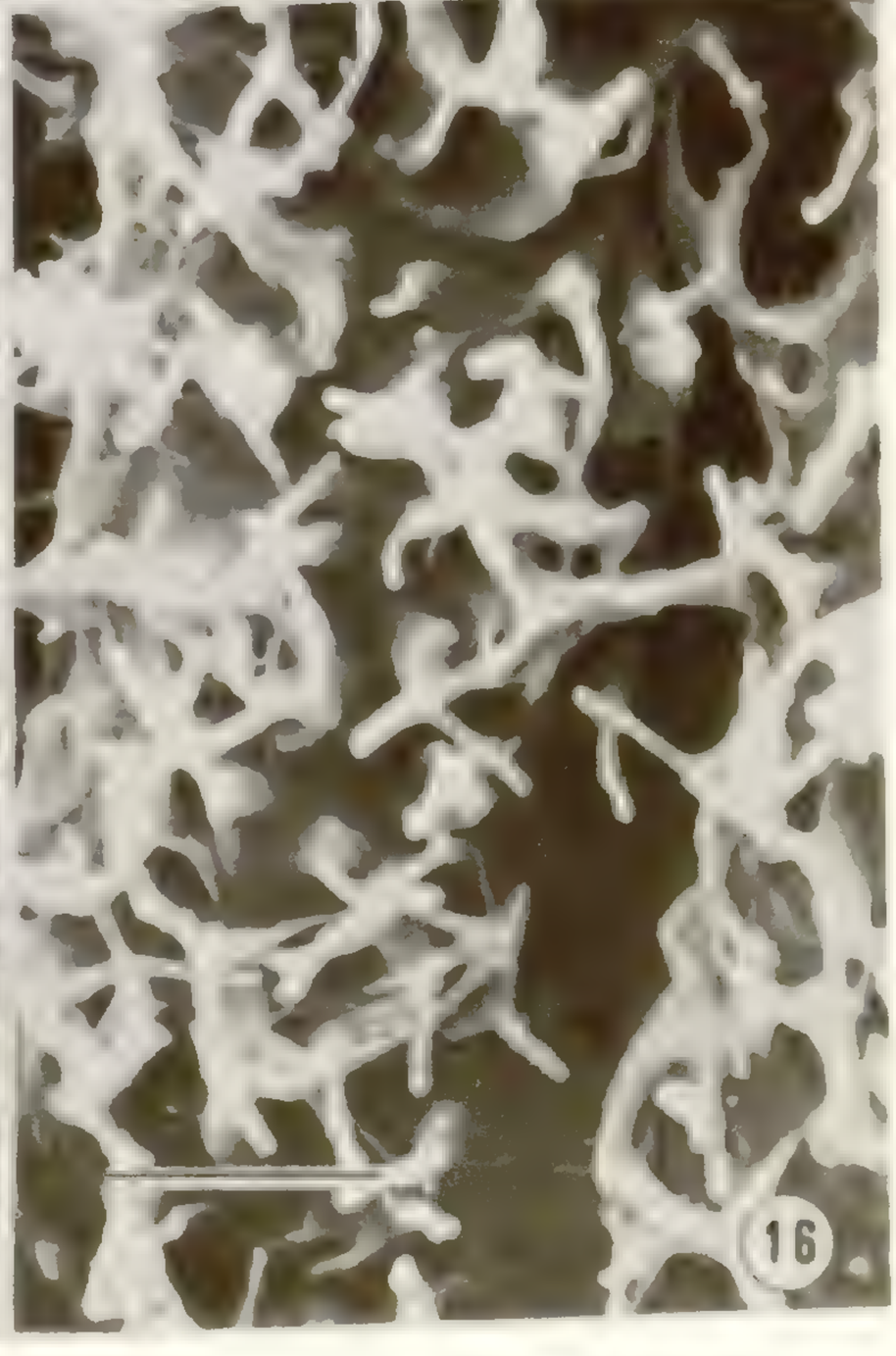
The spores of *A. trichorrhiza* (*Figs. 3, 4,* and *14*) are essentially similar to those of *A. elegans*, except for having generally shorter spines 0.5-1.0 μm long which are much less abundant per unit area of ridge (1-5 μm distant, compared to 0.5-2 μm distant in *A. elegans*). The spores of *A. trichorrhiza* are also generally larger than those of *A. elegans* (ca. 100μm diameter, compared with ca. 60 μm). The trilete scar has little ornamentation and tends to be impressed at its extremities.

The spores of *A. glareosa* (*Figs. 5, 6, 15,* and *16*) have quite distinctive ridge ornamentation. Spines are 0.5-2 μm long and are so dense as to give the spore a puberulent or even floccose appearance. Higher magnification (*Fig. 16*) demon-strates that the spines are often repeatedly forked and occasionally enmeshed. The trilete scar is impressed throughout, which is the most distinctive feature of the species' spores under the SEM.

The spores of *A. ferruginea* (*Figs. 7, 8, 17* and *18*) are nearly identical to those of *A. trichorrhiza*, although Mickel (1962) places the two species in different sections of the subgenus in his treatment, primarily because of differences in the laminae. The ridge spines agree in length and shape with those of *A. trichorrhiza*, but are less distant (0.5-3μm). Higher magnification (*Fig. 18*) suggests a linear or







Details of *Anemia* spores. FIG. 13. *A. elegans* ridges with micropores and bifurcate spines; bar = 4 μm. FIG. 14. *A. trichorrhiza* trilete scar and ridge ornamentation; bar = 10 μm. FIG. 15. *A. glareosa* trilete scar and ridge ornamentation; bar = 10 μm. FIG. 16. *A. glareosa* branched spines; bar = 2.4μm.

Details of *Anemia* spores. FIG. 17. *A. ferruginea* ornamentation; bar = 10μm. FIG. 18. Same; bar = 3 μm. FIG. 19. *A. tomentosa* trilete scar and ridge ornamentation; bar = 6 μm. FIG. 20. *A. rutifolia* trilete scar and ornamentation; bar = 10 μm.

spiral arrangement of spines on the ridges, as well as illustrating two trifurcate spines and several micropores.

The spores of *A. tomentosa* (*Figs. 9, 10,* and *19*) closely resemble those of *A. ferruginea* and *A. trichorrhiza* in all characteristics except ornamentation. In *A. tomentosa* the spines are elongated into obvious hairs up to 6 μm long. Although Mickel (1962, p. 367) noted their occasional absence and doubtful significance, they occurred in all samples examined.

The spores of *A. rutifolia* (*Figs. 11, 12,* and *20*) lack spines on the ridges, although granular irregularities occurred. The strongly raised, trilete scar was distinctive. The absence of ornamentation may be due to the possible immaturity of the spores. However, in contrast to immature grains examined in other samples, these were free rather than in tetrads, which suggests that the spores were mature.

The SEM has allowed the examination of features previously unreported in *Anemia* spores. Simple and branched spines, as well as lax hairs and micropores, can now be seen in detail. Micro-ornamentation of fern spores apparently can be a valuable taxonomic tool. This study suggests a closer relationship between *A. ferruginea* and *A. trichorrhiza* than previously proposed. It also demonstrates that species with very unusual vegetative morphology, *e.g.*, *A. elegans*, are not so unusual with respect to spore morphology. As in the case of higher plants, the conservative nature of spore evolution may indicate the relationship among taxa better than environmentally influenced vegetative variation.

I would like to thank the New York Botanical Garden for allowing my participation in the Planalto expedition. I would also like to thank Dr. E. L. Thurston and Mr. Thomas M. Dreier for their suggestions during the Spring 1976 SEM course at Texas A&M University, and Dr. Paul A. Fryxell for his encouragement and suggestions on the manuscript.

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Experimental Studies on Growth and Sexual Determination in Equisetum Gametophytes

RICHARD L. HAUKE*

The sexual nature of *Equisetum* gametophytes has been problematic for many years and is still not settled. Hauke (1967) and Duckett (1970) gave good reviews of earlier studies on *Equisetum* gametophytes. There is now general agreement that some spores grow into small, sparsely plated,[1] antheridial gametophytes and others into larger, copiously plated, archegonial gametophytes. The latter subsequently produce antheridial lobes, and thus become bisexual (Hauke, 1969; Duckett, 1970, 1972). Antheridial gametophytes are usually shorter-lived than archegonial or bisexual gametophytes. There is a red pigment associated with antheridium formation, either in antheridial gametophytes or in antheridial lobes of bisexual gametophytes (Hauke & Thompson, 1973). LaRoche (1967) disagrees with the interpretation of bisexuality in *Equisetum*. He believes that the gametophytes are dioecious, and vegetatively propagate a second gametophyte generation, which may differ sexually from the first. Davis (1973) states that sex in *Equisetum* is environmentally induced and not genetically fixed, and Duckett (1970) more or less concurs.

In an attempt to understand sexual determination in *Equisetum* gametophytes, various workers have grown them in culture under various conditions (Schratz, 1928; Orth, 1934; Wollersheim, 1957a, b; Hauke, 1968, 1969, 1971; Duckett, 1970, 1972; Ram & Chatterjee, 1970; Davis, 1973). LaRoche (1967) studied *E. arvense* gametophytes grown on various media, with varying pH and other external conditions. His results were expressed in time of development of antheridia, archegonia, and sporophytes, and he never spoke to the relative numbers of one sex or the other. Duckett (1970, 1972) was directly concerned with the percentage of antheridial gametophytes. Using isolated cultures in test tubes, he studied nine different species of *Equisetum* and the influence of three different media on their sexual development. His cultures were maintained for a year or longer. Ram and Chatterjee (1970), using both isolation cultures and mass cultures, studied the effects of pH, percent agar, yeast extract, chemical growth regulators, crowding, varying sucrose concentrations, and light intensity. They reported results as percent male, female, bisexual, or vegetative.

Stephan (1928) apparently was the first to grow *Equisetum* gametophytes on agar in a defined medium. He was also the first to study the effect of light quality and intensity on *Equisetum* gametophyte development. Klebs (1917) earlier had studied the effect of blue and red light on fern gametophyte development (see the review of experimental studies on fern gametophytes by Miller, 1968). Orth (1934) used isolation cultures of *Equisetum arvense* and *E. fluviatile* to test the effect of a

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[1] Duckett (1970) introduced the term "lamella" for the photosynthetic appendages of *Equisetum* gametophytes. I had earlier (1967) adopted the term "plate" for them, following the usage of Kashyap (1914).

female hormone, progynon, on sexual determination. It appeared to increase the percentage of females in *E. arvense*, but not in *E. fluviatile*. In regeneration experiments with male gametophytes, progynon did not convert them to females.

In order to clarify the role of light conditions and nutrient conditions on *Equisetum* sexuality, I have conducted a number of experiments on *E. arvense* and *E. hyemale*, the first member of subgenus *Equisetum* and the second a member of subgenus *Hippochaete*. Some were reported earlier (Hauke, 1971), others are reported here, and some conclusions will be drawn from them.

MATERIALS AND METHODS

The sources of spores used are as follows: *Equisetum arvense* L.—Filled area along ditch, north of Fortin Road, Kingston, Rhode Island, *Hauke 199* (KIRI). *Equisetum hyemale* var. *affine* A. A. Eaton—Brackish marsh among *Phragmites* and *Myrica pensylvanica*, south of Galilee Escape Road, Galilee, Rhode Island, *Hauke 489* (KIRI).

Mature but unopened cones were harvested, washed for 10 min. in 50% "Clorox" to which I had added a drop of detergent per 100 ml, rinsed in three changes of sterile distilled water, then dissected open in sterile distilled water to release the spores. Spores from at least three cones were combined in the spore suspension to eliminate the great variability in sexual expression of spores from different parts of a single cone and from different cones collected at the same time and place (see Duckett, 1970, tables 5, 7). Within each experiment the spore inoculum was uniform, but between experiments great variability was still obtained (i.e. *E. hyemale*, *Tables 8B* and *9*, the former from spores collected on July 12, the latter from spores collected at the same place on September 23). Therefore, when analyzing the data, statistical comparisons were made only within one experiment and never between experiments.

Ten drops of the spore suspension were pipetted onto a petri plate containing ca. 40 ml Bold's Basal Medium solidified with 1.5% agar. This normally resulted in more than 200 spores per culture plate. If the original suspension was very dense, it was diluted with water to keep the number of spores per culture plate below 500.

After treatment, the cultures were tabulated by selecting an area on a petri plate where the gametophytes were sufficiently spaced so that they could be seen as individuals, outlining with a needle on the agar a sufficiently large portion of the culture to yield enough gametophytes for a sample (more than 50), and then picking off the gametophytes under a binocular dissecting microscope at about 30 × to record the sex. If the sex of a gametophyte was doubtful, it was mounted in water on a slide and studied under a microscope at 100 ×. Gametophytes were tabulated as either "male" or "other" because the antheridial gametophytes have a distinctive form, and the antheridia are readily seen. The others might be either archegonial, bisexual, or sterile, Archegonia are hidden among the plates, and so are not seen readily. Experiments were normally terminated before the archegonial gametophytes became bisexual, to avoid the possibility of designating bisexual gametophytes as antheridial. The data are always expressed as "percent

male," meaning the percentage of gametophytes tabulated which were strictly antheridial.

Experiments were terminated when all apparently antheridial gametophytes were sexually mature. This time varied from four to seven weeks, depending on the experiment. To test the effect of continuing an experiment beyond the time when the cultures were judged to be mature, I set up one experiment with two sets of cultures, tabulating one set at maturity (36 days) and the second set two weeks later (*Table 4*). The results did not change significantly.

Cultures usually were grown in a growth chamber under a 12 hr dark-light cycle at 15°C-22°C. The chamber contained eight 40-watt Cool White (Westinghouse) fluorescent tubes and four 25-watt incandescent bulbs. For experiments involving light treatments, petri plates inoculated with *Equisetum* spores were placed in white enamel trays 22 × 36 × 6 cm over which were fitted wooden frames. Cellophane, opaque paper, a holder containing six 4 in^2 glass filters, or cheesecloth (as a neutral filter) were attached to the wooden frame, to create the proper light conditions. For red or blue light, two layers of DuPont "k" 210 FC Red or Blue cellophane were used. These have known transmission spectra (data supplied by DuPont Chemical Co.). For "minus blue" light, Kodak Wratten filter #12 was used, and for blue monochromatic light Kodak Wratten filter #47B was used. These have published spectra.

The red-far red experiments were conducted using monochromatic filters from Carolina Biological Supply Company, CBS Red 650 and CBS Far Red 750. They were placed over incandescent lamps and masked so only light transmitted through the filter reached the cultures being treated.

The amount of radiant energy incident upon the cultures was measured using a YSI Radiometer Model 65, with the sensor placed inside the tray under the filter being used.

Statistical analysis for significance of experimental results utilized a chi-square comparison of number of males versus number of non-males (whether female, bisexual, or without visible sex) on treated versus control plates. An asterisk in the tabulated data indicates statistical significance at the 5% level.

Methods pertinent to individual experiments are described with the specific experiment.

RESULTS AND DISCUSSION

Necessity of light for germination and growth.—Plates were prepared of inorganic medium with or without 0.5% glucose, inoculated with *E. arvense* spores, and placed in trays in a growth chamber, at 20,000 ergs/cm^2/sec light intensity at a temperature of 24° C. One tray was initially covered with opaque paper, a second tray was covered after 1 hour, a third tray after 24 hours, and a fourth tray after 48 hours. The fifth tray was left in the light, which was changed to an 8 hour light-16 hour dark cycle after 48 hours. The experiment was terminated at 20 days. The results (*Table 1*) show that light is necessary for germination of *E. arvense* spores.

To see whether this light requirement for germination applied to other species of *Equisetum*, and to further test its necessity for subsequent growth, a series of

culture plates were prepared, inoculated with spores of *E. hyemale*, and placed in a growth chamber in trays. Some of the trays were immediately covered with opaque paper, others were open to the 12 hour light-dark cycle, at 24°C-16°C, at 10,000 ergs/cm²/sec. After 1 week, 3 weeks, or 5 weeks, plates were transferred from light trays to dark trays. Half of the plates contained media enriched with

TABLE 1. EFFECT OF LIGHT AND GLUCOSE ON GERMINATION AND GROWTH OF *Equisetum arvense* SPORES.

Conditions	*Results*[1]
Dark, no glucose	no germination
Dark, plus 0.5% glucose	no germination
1 hr light, then dark[2]	no germination
24 hr light, then dark	no germination
48 hr light, then dark	germination to the first division, producing one rhizoid
48 hr light, then 8 hr days	normal growth with numerous green cells and rhizoids

[1] After 20 days

[2] All of the light treatments were on medium enriched with 0.5% glucose; Light intensity was 20,000 ergs/cm²/sec.

TABLE 2. EFFECT OF LIGHT AND GLUCOSE ON GERMINATION, GROWTH, AND DEVELOPMENT OF *Equisetum hyemale* GAMETOPHYTES.

Weeks in light[1]	*Weeks in dark*	*0.5% Glucose*	*Observations*[2]		
0	6	–	no germination; spores remain green, appear viable		
0	6	+	as above		
1	5	–	germination, growth to ca. 6 cell stage		
1	5	+	as above, with thin white filament growing from the green gametophyte		
3	3	–	growth to about ca. 15 cell stage		
3	3	+	as above, with thick white filament growing from the green gametophyte		
			Total	*Male*	*% Male*
5	1	–	58	29	50
5	1	+	90	50	55
6	0	–	142	59	42
6	0	+	117	60	51

[1] 12 hr day, at 20,000 ergs/cm²/sec.

[2] Based on 2 or 3 culture plates per treatment.

0.5% glucose. The results, given in *Table 2*, show that light is necessary for germination and growth of *E. hyemale* spores. About 30% of the spores germinated on either medium. Development ceased when partially developed gametophytes were removed from light. Glucose-enriched cultures placed in the dark after 1 or 3 weeks did develop a white, filamentous structure several cells long from the immature green gametophyte, but did not continue normal gametophyte growth. There was no significant difference between gametophytes in light for 5 weeks and those in light for 6 weeks, nor was there any between cultures enriched with glucose and those not so enriched.

The necessity of light for germination and growth of *Equisetum* spores is not negated by glucose enrichment. That the glucose is taken up is indicated by the production of abnormal growth in gametophytes placed in the dark after one or three weeks in the light. Thus, I assume that the role of light in germination of *Equisetum* spores and growth of the gametophytes is not just a nutritional (photosynthetic) one. Schulz (1901) first pointed out the necessity of light for germination of *Equisetum* spores, but thought that since these spores contain no stored food the role of light was solely photosynthetic. Wollersheim (1975b) claimed that spores could germinate in the dark. He inoculated some plates, placed them in the dark, and observed them every 5 days in the light. After 30 days the spores had divided, but the rhizoid cell did not grow out. If brought into the light, even up to 2 months later, they would grow. If *Equisetum* gametophytes operate on the reciprocity law (see below), then spores exposed to the light every 5 days possibly could absorb enough photons after five or six exposures to permit the first division to occur. Wollersheim also reported that gametophytes at the 3 or 4 cell stage ceased further development when placed in the dark. Ram and Chatterjee (1970) claimed that spores of *E. ramosissimum* subsp. *ramosissimum* germinated in the dark and grew to a 7-celled, yellow filament. Their experimental conditions weren't clearly stated, but they apparently studied the cultures twice a week under a dissecting microscope for 12 weeks, and their cultures were on medium enriched with 0.5% sucrose.

The necessity of light for germination of fern spores has been extensively studied (Miller, 1968), and in at least one case *(Anemia),* GA can induce germination in the dark. Since most fern spores are non-green, resistant structures containing stored food, their requirement of light for germination generally has not been considered photosynthetic.

Effect of day length on sexuality.—Experiments were set up to see whether the light duration was important in sex determination of *Equisetum*. Plates inoculated with *E. hyemale* spores were placed under either an 8 hr light–16 hr dark cycle or a 16 hr light–8 hr dark cycle. In either case, some cultures were subjected to white light and others to red light. Plates inoculated with *E. arvense* spores were placed under either an 8 hr light–16 hr dark cycle or under a 12 hr light–dark cycle. In either case, some plates contained only inorganic medium and others contained medium enriched with 0.5% glucose. Intensity was set at 20,000 ergs/cm^2/sec. The results of these experiments (*Table 3*) were that *E. hyemale* under white light showed no difference between 8 and 16 hr days in percent of antheridial gametophytes, but under red light an 8 hr day was more effective than a 16 hr day in inducing male gametophytes. In both cases, red light was significantly more effective than white light in producing male gametophytes. *Equisetum arvense* developed significantly more male gametophytes under a long than under a short day, but this effect was negated by glucose enrichment. The effect of longer day length in *E. arvense* is consistent with the effect of higher light intensities on sexuality in *E. arvense,* as reported previously (Hauke, 1971), under the reciprocity law (Law of Photochemical Equivalence), which states that the light effect is

cumulative. This is understood in terms of the total quanta of light received, whether at high intensity for a short time, or at lower intensity for a longer time. Haupt (1957), in his studies of induction of polarity in *Equisetum* spores by light, reported that this was a "dose response" phenomenon, another way of saying that it followed the reciprocity law.

TABLE 3. EFFECT OF DAY LENGTH ON SEXUALITY OF *Equisetum* GAMETOPHYTES.

Species	*Conditions*[1]	*Age (days)*	*Total*[2]	*Males*	*% Male*
E. hyemale	16 hr day, white light	43	356	63	18
	16 hr day, red light	43	541	133	25*
	8 hr day, white light	49	131	23	18
	8 hr day, red light	49	348	220	63*
E. arvense	12 hr day	35	253	239	94*
	12 hr day, +0.5% glucose	35	200	193	97*
	8 hr day	35	232	164	71
	8 hr day, +0.5% glucose	35	181	164	91*

[1]Light intensity for *E. hyemale* 16,000 ergs/cm²/sec, for *E. arvense* 20,000 ergs/cm²/sec.
[2]Based on 2 or 3 culture plates per treatment.

TABLE 4. EFFECT OF THE ABSENCE OF BLUE LIGHT ON SEXUALITY OF *Equisetum hyemale* GAMETOPHYTES.

Light[1]	*Duration (days)*	*Total*[2]	*Males*	*%Male*
White	36	278	145	52
Red	36	289	182	63*
−Blue	36	304	196	64*
White	50	260	135	52
Red	50	260	170	65*
−Blue	50	285	190	67*

[1]Intensity of white, 12,000 ergs/cm²/sec; of red, 14,000 ergs/cm²/sec; of −blue, 15,000 ergs/cm²/sec.
[2]Based on 3 culture plates per treatment.

Light quality in E. hyemale sex determination.—Red light has been shown to increase the percentage of male gametophytes in cultures of *E. hyemale* (Hauke, 1971). To determine whether that was the result of the presence of red wavelengths or the absence of blue wavelengths, an experiment was set up consisting of three sets of six plates each, one covered with red cellophane (transmitting more than 80% in the red part of the spectrum, less than 5% in the blue), one with filters excluding the blue part of the spectrum (no transmission below 500 nm), and the third exposed to white light. Intensities were adjusted to be approximately the same; 14,000 ergs/cm²/sec under red, 15,000 ergs/cm²/sec under blue, and 12,000 ergs/cm²/sec under white. The results, given in *Table 4*, with either the presence of red light or the absence of blue light were the same: a significant increase in the number of male gametophytes. It appears that the red light effect in *E. hyemale* sexuality is actually a response to the absence of blue light.

The red–far red system.—Since red-far red systems have such widespread developmental effects among plants, experiments were conducted to determine whether such a phytochrome system might be operative in *Equisetum* sex determination. Both *E. hyemale* and *E. arvense* were grown under an 8 hr light–16 hr dark cycle, with the middle of the dark period interrupted by far-red light, or far-red followed by red light for 1 minute each. In another experiment, *E. hyemale* was grown under a 16 hr light–8 hr dark cycle, with the light period immediately followed by 5 min of far red light, or far red followed by 5 min of red light.

TABLE 5. EFFECT OF FAR RED LIGHT ON SEXUALITY IN *Equisetum* GAMETOPHYTES.

Expt.	*Species*	*Conditions*[1]	*Total*[2]	*Male*	%Male
A	E. hyemale	control	148	3	2
		far red	194	6	3
		far red + red	163	2	1
B	E. hyemale	control	287	28	10
		far red	282	18	6
		far red + red	288	26	9
C	E. arvense	control	232	164	71
		control + glucose	181	164	91*
		far red	339	262	77
		far red + glucose	80	72	90*
		far red + red	167	130	78
		far red + red + glucose	168	160	95*

[1] Expt. A: 16 hr light-8 hr dark cycle, light followed by 5 min far red, or 5 min far red followed by 5 min red light. Treatment started 15th day, experiment terminated 29th day. Light intensity 12,000 ergs/cm^2/sec.

Expt. B and C: 8 hr light-16 hr dark cycle, middle of dark period interrupted by 1 min far red, or 1 min far red followed by 1 min red light. Treatment started 1st day, experiment terminated 35th day. Light intensity for B 16,000 ergs/cm^2/sec; for C 20,000 ergs/cm^2/sec.

[2] Expt. A based on 6 culture plates per treatment. Expt. B and C based on 2 or 3 culture plates per treatment.

No effect of treatment with far red light was seen (*Table 5*). These results are consistent with those of another experiment using interruption of the dark period with 2 hours of white light, which had no effect on the sexuality of either *E. hyemale* or *E. arvense* (*Table 6*).

The blue light system.—In an experiment (*Table 6*) in which plants grown on an 8 hr light–16 hr dark cycle under blue light (filtered through blue cellophane) developed normally, those grown under the same conditions, but with the dark period interrupted by 2 hours of light from an incandescent bulb, displayed a marked inhibition of development. Earlier experiments (Hauke, 1971) had shown no effect of blue light quality on either *E. arvense* or *E. hyemale* sex determination. In an attempt to determine whether or not a blue light photomorphogenic system is operative in *Equisetum* gametophyte development, an experiment was set up using *E. arvense* with four sets of cultures. All were on a 12 hr light–dark cycle. One set had 5 minutes of white light in the middle of the dark period, one had 5 minutes of blue enriched light (filtered through blue cellophane), and one

had 5 minutes of blue monochromatic light (filtered through a Kodak Wratten 47B filter, transmitting between 400 and 500 nm, with the majority of the light from 420 to 470 nm). The fourth set had no interruption of the dark period. The results of this experiment (*Table 7*) were that the cultures given 5 minutes of blue light during the dark period, whether monochromatic or enriched, had significantly fewer male gametophytes than those given white light or no light.

TABLE 6. EFFECT OF INTERRUPTION OF DARK PERIOD BY TWO HOURS OF LIGHT ON SEXUALITY IN *Equisetum* GAMETOPHYTES.

Species	*Light*[1]	*Dark period*[1]	*Age (days)*	*Total*[2]	*Male*	*% male*
E. arvense	white	continuous	43	253	112	44
	white	interrupted	43	182	82	45
	blue	continuous	50	85[3]	58	68*
	blue	interrupted	50	sexually undeveloped		
E. hyemale	white	continuous	43	140	61	44
	white	interrupted	43	128	51	40
	blue	continuous	50	161	76	47
	blue	interrupted	50	sexually undeveloped		

[1] 8 hr light-16 hr dark cycle, with 2 hr interruption in middle of dark period provided by incandescent light. Blue light filtered through cellophane. Light intensity 10,000 ergs/cm^2/sec.
[2] Based on 2 culture plates per treatment, except where indicated.
[3] Based on 1 culture plate.

TABLE 7. EFFECT OF INTERRUPTION OF DARK PERIOD BY 5 MINUTES OF WHITE OR BLUE LIGHT ON SEXUALITY IN *Equisetum arvense* GAMETOPHYTES.

Treatment[1]	*Total*[2]	*Male*	*% Male*
Dark period uninterrupted	682	310	45
Dark period interrupted with white light	478	229	47
Dark period interrupted with blue enriched light (blue cellophane)	664	254	38*
Dark period interrupted with blue monochromatic light (glass filter)	674	261	38*

[1] All on 12 hr light-dark cycle. Treatment started 8th day; experiment terminated 35th day. Light intensity 12,000 ergs/cm^2/sec, fluorescent only.
[2] Based on 5 or 6 culture plates per treatment.

A blue light morphogenic system does appear to be present in *Equisetum*. Blue light morphogenic systems are apparently widespread. The importance of blue light in fern gametophyte growth has been reviewed by Miller (1968). The effects of blue light in surpressing etiolation and in controlling flowering in angiosperms have been studied (see Schneider et al, 1967). Haupt (1957) reported that blue light was the most effective in inducing polarity in *Equisetum* spores. That it might be a High Energy Reaction (HER) system is suggested by the slight, although statistically significant, decrease in maleness seen under treatment in *Table 7*, as compared to the very strong inhibition of development with a two hour night time interruption seen in *Table 6*. In the first experiment reported here (*Table 6*), with two hours of incandescent light filtered through blue cellophane, it is quite possible that an HER system with peaks in the blue and far-red regions of the spectrum is operative (see Leopold & Kreidman, 1975).

Effect of isolation on sexuality.—A series of experiments was set up in which, after the initial inoculation into culture dishes and after germination had become detectable, germinated spores were transferred into tubes, one per tube. In this way the interaction of gametophytes on one another, either by competition for nutrients or by interference from metabolic products, could be detected. From such experiments (*Table 8*), it appears that there is a tendency for isolated gametophytes to become male less often than those in mass culture. Sucrose enrichment of *E. arvense* mass cultures decreased the percentage of males, whereas it had no effect on isolated cultures. Gametophytes in isolation grew considerably larger than those in mass culture, and females in isolation took much longer to become bisexual than did those in mass culture (in one case they remained unisexual after 260 days).

Duckett (1970) found up to 97% males in isolated cultures of *E. arvense*, and reported that one female only became bisexual after 280 days.

TABLE 8. EFFECT OF ISOLATION ON SEXUAL DEVELOPMENT OF *Equisetum* GAMETOPHYTES.

Expt.	*Species*	*Conditions*[1]	*Total*	*Male*	*% Male*
A	E. hyemale	tube	23	7	30
		tube + 0.5 sucrose	24	4	17
		plate	151[2]	21	14
		plate + 0.5% sucrose	201[2]	27	13
B	E. hyemale	tube	23	4	17*
		plate	260[3]	135	52
C	E. arvense	tube	20	11	55*
		tube + 0.5% sucrose	22	11	50*
		plate	114[3]	95	83
		plate + 0.5% sucrose	109[3]	52	48*

[1]Expt. A: 10,000 ergs/cm²/sec for 35 days.
Expt. B: 12,000 ergs/cm²/sec for 36 days.
Expt. C: 11,000 ergs/cm²/sec for 46 days.
[2]Based on 2 culture plates each.
[3]Based on 3 culture plates each.

Effect of reused medium.—The possibility of diffusible metabolic products affecting sexual development was explored. I conducted an experiment using medium upon which *Equisetum* gametophytes had been grown to sexual maturity. Gametophytes of *E. hyemale* were grown for 2 months on plates, then removed and the medium was autoclaved and new plates poured from it. These were inoculated with spores of *E. hyemale*, as were plates of newly prepared medium. Six plates of each were prepared, but germination was much greater on reused medium than on fresh medium. Consequently, the numbers tabulated for reused medium are higher than those for the fresh medium. In this experiment all gametophytes on a plate were sexed, but without removing them from the plate, so that the effect of prolonged culture could be determined.

The results, given in *Table 9*, show that there is nothing comparable to the antheridogen of ferns in *Equisetum*. Gametophytes on both fresh and reused

medium displayed the same sexual expression. However, gametangia were observed earlier on gametophytes growing on the reused medium (at 21 days), gametophyte growth was more luxuriant, and as the cultures aged it was observed that by 45 days there was a great difference between them, in that most of the gametophytes on reused medium were bisexual whereas most of those on fresh medium were female. The reused medium did not affect initial sexuality, but did hasten the transition from female to bisexual. This is consistent with the observation made in the isolation experiments, where isolated females took much longer to become bisexual than did those in mass culture.

TABLE 9. EFFECT OF REUSED MEDIUM ON SEXUALITY IN *Equisetum hyemale* GAMETOPHYTES.

Medium[1]	*Total*[2]	*Male*	*% Male*
Fresh	148	3	2
Reused	1035	31	3

[1]Light conditions were a 16 hr day at 12,000 ergs/cm²/sec.
[2]Based on 6 culture plates per treatment. Germination on fresh medium was ca. 10%, on reused medium ca. 90%.

TABLE 10. EFFECT OF MINERAL NUTRITION LEVEL ON SEXUALITY IN *Equisetum arvense* GAMETOPHYTES.

Light intensity[1]	*Medium concentration*	*Total*[2]	*Male*	*% Male*
4000	1	314	219	70
	1/2	239	172	72
	1/10	306	290	95*
	1/20	260	253	97*
3200	1	417	316	76
	1/2	184	132	72
	1/10	291	237	81[3]
	1/20	323	265	82*

[1]Ergs/cm²/sec, 12 hr day.
[2]Based on 3 culture plates per treatment.
[3]Chi-square = 3.2; .10>P>.05.

Comparison of cultures of gametophytes isolated in test tubes and in mass cultures revealed some interaction between gametophytes. The more luxuriant growth of gametophytes in tubes was most likely the result of the absence of some gametophyte interaction. This might be competition for mineral nutrition, which is unlikely since as seen in *Table 10* even medium diluted to half strength was sufficient to support normal growth. It might be the production of some allelopathic substance. The darkening of the medium near gametophytes in tubes does seem to show that some substance is being secreted into the substrate by the gametophytes. Duckett's work (1970, 1972), in which with many species he obtained more than 50% males in his isolation cultures, casts doubt on the possibility that there is an antheridogen system, as has been detected in some ferns (see Miller, 1968). The results in *Table 9* further substantiate the absence of antheridogens, but the observations made subsequently raised the possibility of another

type of diffusible substance affecting sexual determination. As Duckett has so clearly shown (1970, 1972), initially archegonial gametophytes eventually all become bisexual, but at differing rates dependent upon the species. I have further noticed that isolated females in test tubes take longer to become bisexual than those in mass culture. Medium upon which gametophytes had been previously growing hastened the appearance of antheridia on archegonial gametophytes, over that seen in gametophytes growing on fresh medium. All of these observations suggest the presence in the substrate of some substance given off by gametophytes and affecting sexual expression of the gametophytes. Ram and Chatterjee (1970) postulated a similar substance.

Dilution of the medium.—To determine whether the level of mineral nutrition might influence sexuality, an experiment was set up using the standard medium and medium diluted to 1/2, 1/10, or 1/20 normal strength. Two series of *E. arvense* were grown, one at 4000 ergs/cm^2/sec and the other at 3200 ergs/cm^2/sec. The results (*Table 10*) did indicate a significant effect of the more dilute medium (1/10, 1/20), which induced a higher percentage of maleness at the higher light intensity. At the lower intensity, the more dilute media also bore more antheridial gametophytes, but the 1/10 dilution was only marginally significant with the chi-square test. Visually, the gametophytes on more dilute medium at higher light intensity were smaller and more yellowish than the others.

The last set of experiments reported above, on the effect of dilution of the medium on sexual development of *E. arvense*, suggests that a mineral nutrient deficiency does indeed increase percentage of maleness, as has been long assumed. At half strength, growth wasn't affected. LaRoche (1967) reported that Knop's medium at half to quarter strength was better than at full strength, but half strength Knop's has about the same amount of mineral nutrients as full strength Bold's medium. On more dilute media (1/10 and 1/20), there was an increase in the number of antheridial gametophytes, which was exacerbated by a slight increase in light intensity that was insufficient to affect the sexual development of cultures at higher nutrient levels.

Effect of sugar enrichment.—Earlier I reported that sucrose enrichment affected the sexuality of *Equisetum* gametophytes, but that this effect did not appear to be nutritional (Hauke, 1971). Glucose enrichment did not affect sexual expression in *E. hyemale (Table 2)*, but it did increase the number of male gametophytes in *E. arvense (Table 5)*. Castle (1957) reported that sucrose above 5,000 mg/l caused early necrosis of the gametophytes, which he attributed to hastened growth and subsequent exhaustion of some essential element in the medium, or to the accumulation of toxic substances in the medium. Wollersheim (1957b), using *E. limosum (E. fluviatile)*, found that 2% glucose caused an increase in the number of female gametophytes to 90%, versus 75% on unenriched Knop's medium. Ram and Chatterjee (1970), using 1% to 4% sucrose, found that archegonial development was supressed at higher concentrations, but the percentage of antheridial gametophytes was not changed. Their experiments were conducted at very low light levels (15 ft-c for 11 hrs) under which in the absence of sucrose gametophyte

growth was "highly restricted." In one experiment I conducted with *E. hyemale*, 1% glucose caused malformation and necrosis of the gametophytes, whereas 0.5% glucose did not affect either the growth or the sexual expression. A number of experiments utilizing sugar enrichment were attempted, but the results were so inconsistent that no conclusions can be drawn from them.

GENERAL DISCUSSION

The basis for sexual determination in *Equisetum* gametophytes is still unclear. The general assumptions were that *Equisetum* gametophytes are inherently bisexual, that nutritional and other environmental conditions determine the sex of gametophytes at an early stage, and that once determined, the sex is usually maintained but can be reversed (Hauke, 1967). Duckett (1970) found variation among species, but concluded that in general, conditions favoring vigorous vegetative growth (e.g., high light intensities) produced more initially female individuals, whereas less favorable regimens (e.g., high temperatures) fostered male gametophytes. (He did not present data of culture under various light regimens.) That still does not answer the question: why, under exactly the same conditions, do some spores develop into male gametophytes, others into female? Schedlbauer (1976) reported that in the Water Fern, *Ceratopteris thalictroides,* there is a positive correlation between spore size and gametophyte growth. Since the first gametophytes become bisexual and by antheridogen production induce the slower-growing gametophytes to become male, smaller spores grow into antheridial gametophytes. However, the apparent analogy in *Equisetum* in which the more vigorously vegetative gametophytes become archegonial and eventually bisexual, is misleading. There is no anteridogen system operating here, and the first gametophytes to mature sexually are the antheridial ones. In *Ceratopteris,* isolated gametophytes become bisexual, that is, all develop the same under similar conditions, whereas in *Equisetum,* even under what seem to be favorable conditions for vegetative growth, some isolated gametophytes develop as males.

Light, nutritional, and other environmental conditions affect the sex ratio in *Equisetum,* but they do not appear to be the complete answer. Hauke (1967) postulated a sort of relative sexuality of spores and (1969) a transition within *Equisetum* "from a primitively bisexual condition to a stable unisexual condition through an intermediate plastic unisexuality." LaRoche and Vo-thi-Dao (1972) speculated that "les spores d'*Equisetum arvense* sont unisexuées, le sexe femelle serait neutre d'où sa capacité d'expression en l'absence de toute influence mâle." Ram and Chatterjee (1970) think that "the condition presented by *Equisetum* shows the beginning of heterospory." All of these speculations imply a genetic basis of some sort for sex in *Equisetum* spores.

CONCLUSIONS

1. Light is necessary for germination and growth of *Equisetum* gametophytes, and glucose enrichment does not replace the light requirement.

2. Day length is not a factor in *E. hyemale* sexual expression, and in *E. arvense* the effect of longer day length is probably a total light energy effect, rather than a duration effect.

3. The effect of red light on sexual expression of *E. hyemale* is in fact the effect of the absence of blue light.

4. There does not appear to be a red-far red light system operating in spore germination and growth in *Equisetum*.

5. There does appear to be a blue light system operative in *Equisetum*.

6. There is some type of interaction between *Equisetum* gametophytes, but it is apparently via a diffusible metabolic product other than an antheridogen.

7. Mineral nutrition can be critical in *Equisetum* gametophytes, but standard culture media have at least twice as much mineral content as is necessary.

8. The basis of sexual determination in *Equisetum* gametophytes is still unclear.

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SHORTER NOTES

THE AZTECA ANTS OF SOLANOPTERIS BRUNEI.— The Potato-ferns, *Solanopteris,* have been known not only for their tubers, which are modified secondary rhizomes, but also for their frequent (if not constant) association with ants, which often hinder collecting the ferns. The original material of *Solanopteris*, which was sent to Hooker and described by him as *Polypodium bifrons*, was annotated by its collector, Jameson, as being inhabited by very obnoxious ants. Almost all subsequent collections of the various species of *Solanopteris* have been reported with ants.

These insects can play an important role in the biology of the fern,[1] but no pteridologist has ever tried to learn which species of ants are found with it. Of the ant genera *Camponotus, Pheidole, Solenopsis* and *Azteca*, the latter is always present in the Costa Rican *Solanopteris brunei* (Wercklé in Christ) Wagner. Comparison with other *Azteca* species known in Costa Rica proved useless: the fern ant was something different. Although the taxonomy of *Azteca* is in urgent need of revision, a publication[2] dealing with myrmecophilous plants and their ants in South America has come to my attention which describes on page 692 *Azteca traili* var. *filicis* Forel, from Cerro de Ponasa, Peru. These ants inhabit "a Polypodium-like fern with tubers in the fashion of *Myrmecodia*, on a *Tococa* tree with ant gardens." The plant so described by E. Ule is undoubtedly a species of *Solanopteris,* possibly *S. bifrons*. Costa Rican ant specimens sent to Walter Kempf, myrmecologist at the University of Brasilia, were identified as the ant described by Forel, although somewhat larger than the typical Peruvian forms.

The presence of a South American insect as far north as Costa Rica, to date the northernmost range of *Solanopteris,* implies that both the ants and the ferns have coevolved, not only in their intimate biological relationships, but also along a common geographical range. It would be interesting to know if the ants inhabiting *Solanopteris* species other than *S. brunei* are the same species or not.—*Luis Diego Gómez, Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

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[1] Gómez P., L. D. 1974. Biology of the potato-fern Solanopteris brunei. Brenesia **4:** 37-61.

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The Genus Botrychium (Ophioglossaceae) in Arizona

TIMOTHY REEVES*

This article updates the treatment of the genus *Botrychium* Swartz (Grape Ferns and Moonworts) in Arizona and provides a key and illustrations as an aid to their identification. The most recently published key including all the species of *Botrychium* found in Arizona is that in the monographic treatment of the Ophioglossaceae by Clausen (1938). Four species of *Botrychium* have been reported previously from Arizona: *B. lanceolatum, B. lunaria* (San Francisco Peaks), *B. multifidum* (White Mountains), and *B. virginianum* (Santa Rita Mountains) (Maxon, 1942; Phillips, 1946–1947; Morton, 1951).

The examination of extensive field collections of botrychiums in Arizona and of specimens in five Arizona herbaria (ARIZ, ASC, ASU, ASUF, and MNA) has revealed additional records for the State. All specimens examined by me are cited in the following checklist. Three additional specimens cited by previous authors but not examined by me are also included.

Botrychium boreale, B. dissectum f. *obliquum,* and *B. dusenii* are reported here as new to Arizona. Second localities within the State for *B. lanceolatum, B. lunaria,* and *B. multifidum* are based upon collections from the White Mountains. These reports for the three taxa new to Arizona represent considerable range extensions for each species. *Botrychium boreale* was previously known only as far south as northern Nevada (Cronquist et al., 1972), northern Utah (Flowers, 1944), and northern Colorado (Weber, 1966), over 600 km north of the Arizona localities. This report of *B. dissectum* f. *obliquum* represents a westward range extension of 1370 km from known stations in eastern Kansas (Petrik-Ott, 1975). I have examined a collection of *B. dusenii* from Charleston Peak, Clark County, Nevada (*Clokey & Ely* in 1937, ASU), which is about 300 km west of the San Francisco Peaks locality.

The richest areas in Arizona for botrychiums are the two highest mountains, the San Francisco Peaks and Mount Baldy *(Fig. 8).* On the San Francisco Peaks, botrychiums are quite common from 2900 to 3550 m elevation. They are most plentiful in the meadows of the Inner Basin (2900–3100 m), where *B. boreale, B. dusenii, B. lunaria,* and *B. lanceolatum* occur together. The meadows are surrounded by a spruce-aspen forest. Large logs (presumably the result of a forest fire many years ago) are scattered over the undulating, rocky terrain. *Juniperus communis, Lonicera involucrata,* and *Ribes* sp. are common shrubs. Herbaceous angiosperms include *Anemone globosa, Arenaria fendleri, Carex* spp., *Castilleja linariifolia, Fragaria ovalis, Lathyrus arizonicus, Poa fendleriana, Potentilla pulcherrima, Pseudocymopteris montanus, Solidago decumbens, Solidago multiradiata, Swertia radiata,* and *Zigadenus elegans. Cystopteris* is the only other

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fern present. I have observed hundreds of plants of *Botrychium* here, and all species are common except *B. dusenii*.

Three species of *Botrychium* occur at Fremont Saddle (between Doyle Peak and Fremont Peak of the San Francisco Peaks at 3292 m), where scattered Bristlecone Pine and spruce trees are found. Associated angiosperms include *Androsace septentrionalis, Arenaria lanuginosa, Lupinus argenteus, Penstemon whippleanus,* and *Pseudocymopteris montanus*.

The highest known elevation occurrence of *Botrychium* in Arizona is on Agassiz Peak of the San Francisco Peaks at 3550 m near timberline. Here *B. lunaria* is uncommon, growing in dense herbaceous vegetation in open areas of scattered spruce krummholz. *Geum turbinatum* is the dominant ground cover. Associated herbaceous species represented are *Arenaria rubella, Festuca ovina, Mertensia franciscana, Polemonium viscosum, Pseudocymopteris montanus, Ribes montigenum, Saxifraga flagellaris, Saxifraga rhomboidea, Sedum rhodanthum, Sibbaldia procumbens, Silene acaulis,* and *Solidago multiradiata*.

Four species of *Botrychium* are found on Mount Baldy in the White Mountains. *Botrychium boreale* is the most abundant species. *Botrychium dusenii, B. lanceolatum,* and *B. lunaria* are also present. *Botrychium dusenii,* which is rare on the San Francisco Peaks, is rather common on Mount Baldy. Here, the four species are scattered throughout the grassy subalpine bald, at least from 0.5-0.7 km NNW of the summit of Baldy Peak (3425 m). Associated species include *Achillea lanulosa, Arenaria fendleri, Draba helleriana, Festuca ovina, Heuchera parvifolia, Pedicularis parryi, Potentilla diversifolia, Pseudocymopteris montanus, Sedum rhodanthum, Solidago parryi,* and *Zygadenus virescens*.

The climates of the San Francisco Peaks and Mount Baldy are quite similar. Both mountains lie in the Plateau section of Arizona *(Fig. 8),* as delimited by Sellers and Hill (1974). This portion of the State is characterized by high annual precipitation and low temperatures as compared with most of the rest of Arizona. The higher portions of the San Francisco Peaks receive about 889 mm (35 in.) of precipitation annually (Smith, 1974). Mount Baldy probably receives a comparable amount since the nearby weather station in the Phelps Cabin Research Natural Area, although 600 m lower in elevation than Mount Baldy, receives about 711 mm (28 in.) per year (Smith, 1974). The average January temperatures for both mountains are below −4°C (25°F), and the average July temperatures are below 15.5°C (60°F), according to Sellers and Hill (1974). The average daily maximum temperature-humidity index in July is between 70 and 75 (Sellers & Hill, 1974). One can expect botrychiums growing in open areas at higher elevations on the Kaibab Plateau (ca. 150 km NNW of the San Francisco Peaks), where there is a similar climatic regime.

The habitats of all botrychiums growing at the higher elevations in Arizona have much in common. All specimens I have collected were growing in open, sunny mountain balds or meadows. The soil was often devoid of competing vegetation, at least in the immediate vicinity of the botrychiums. On Mount Baldy, the soil is apparently affected by freeze-thaw activity, and the botrychiums are most prevalent in barren, gravelly spots or growing through mats of lichens or mosses. In the

Inner Basin on the San Francisco Peaks, the plants are most abundant in open, gravelly soil or in spots covered by leaf litter. Although some botrychiums do occur in close association with other herbaceous vegetation, the prevalence of bare ground at these sites seems significant.

Except for *B. dissectum* and *B. multifidum*, Arizona botrychiums are winter deciduous. Consequently, collections must be made in summer months. Most of the specimens cited in this article were collected in July and August. Most specimens, even those collected in early July, had mature spores.

Care must be taken in preparing *Botrychium* specimens, especially those of subgenus *Botrychium*, which have subtle characters. It is desirable, after "taming" the freshly collected specimens in the press, to open the press and carefully tease out the segments so that they resemble those of living plants and are not folded together.

KEY TO BOTRYCHIUM IN ARIZONA

1. Stalk of sterile blade 1.5–8.0 cm long, inserted near the base of the plant (subg. *Sceptridium*).
   2. Plant fleshy; stalk of sterile blade 1.5–5.0 cm long; common stalk of sterile and fertile blades ≥0.5 cm in diameter; ultimate divisions of sterile blade rather uniform in size, the pinnae regularly divided to near the apex; segments overlapping, or not, obtuse at the apex.
      1. *B. multifidum* var. *intermedium*
   2. Plant not or only slightly fleshy; stalk of sterile blade 5.5–8.0 cm long; common stalk ≤0.3 cm in diameter; ultimate divisions of sterile blade of various sizes, the pinnae not truly pinnate in the distal 1/3–1/4; segments not or only slightly overlapping, the larger segments acute at the apex.
      2. *B. dissectum* f. *obliquum*

1. Stalk of sterile blade 0–1.5 cm long, inserted near the middle of the plant or higher.
   3. Plants ≥30 cm tall; sterile blade tripinnate or more divided, up to 20 cm wide at the base (subg. *Osmundopteris*) ..... 3. *B. virginianum*
   3. Plants ≤20 cm tall; sterile blade pinnate to bipinnate, up to 4 cm wide (subg. *Botrychium*).
      4. Sterile blade sub-bipinnate (at least basally) to bipinnate; common stalk of fertile and sterile blades often yellow-brown to red-brown abaxially.
         5. Sterile blade sessile, as wide as long; common stalk deep red-brown; lowest basiscopic pinnule usually greatly enlarged; segments not overlapping; both fertile and sterile blades deflexed in bud. ..... 4. *B. lanceolatum* var. *lanceolatum*
         5. Sterile blade sessile to stalked, longer than wide; common stalk often yellow-brown; lowest basiscopic pinnule not greatly enlarged; segments often overlapping; both fertile and sterile blades erect in bud ..... 5. *B. boreale*
      4. Sterile blade pinnate; common stalk usually green.
         6. Plants ≤8.5 cm tall; segments of sterile blade about as wide as long, ≤0.5 cm wide, often spatulate and distinctly petioled, sometimes cuneate, often crenate ..... 6. *B. dusenii*
         6. Plants to 20 cm tall; segments of sterile blade usually wider than long, to 1.5 cm wide, flabellate and apically rounded, entire or incised, nearly sessile or cuneate to a broad petiole.
            7. *B. lunaria*

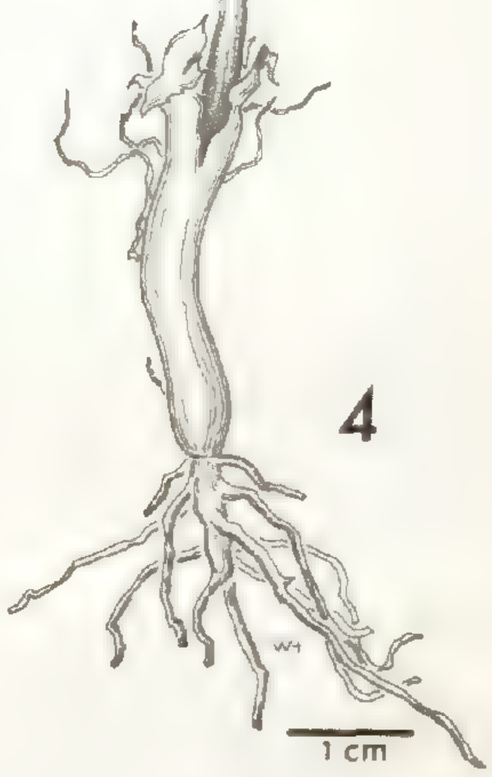
1. B. multifidum var. intermedium (D. C. Eat.) Farw. Leathery Grape Fern. Fig. 1.

APACHE CO.: White Mountains, Fort Apache Indian Reservation, Diamond Creek Beaver Dams, 24–32 km NE of Whiteriver, grassy flat or upland meadow near upper limit of the ponderosa pine zone, 2438 m, *Goodding & Schroeder 340-41* (ARIZ, ASU); Maverick Cienega, ca. 8 km S of Hawley Lake, opening at edge of aspen-spruce-ponderosa pine forest, growing in bare or litter (aspen leaves) covered soil at edge of open meadow. Associated with *Aconitum columbianum*, *Pteridium aquilinum*, *Viola canadensis*, *Veratrum californicum*, and grasses; 2560 m, *Reeves 5305* (ASU).

3
1 cm

2
1cm

1 cm


4
1 cm

1
1cm

5a
1cm

5b
1 cm

In late July, the plants are small with the fertile and sterile blades of the present season unfolding, and the previous season's sterile blade still green and lying flat on the ground.

2. B. dissectum f. obliquum (Muhl.) Fern. Cutleaf Grape Fern. Fig. 2.

GILA CO.: Pinal Mountains, Pinal Creek, 1981 m, 25 Aug 1915, *Anna Jackson* (ASU).

According to W. H. Wagner, Jr. (pers. comm.), who has examined this collection, the specimens are remarkably like those found in the eastern United States in size, pinnule outline, and cutting. They do not resemble the Mexican and Guatemalan *B. dissectum* subsp. *decompositum* (Mart. & Gal.) Clausen.

3. B. virginianum (L.) Swartz Rattlesnake Fern. Fig. 6.

SANTA CRUZ OR PIMA CO.: Santa Rita Mountains, 6 June 1884, *Pringle* (Photo of GH specimen, ARIZ).

4. B. lanceolatum (Gmel.) Ångstr. var. lanceolatum. Lanceleaf Grape Fern. Fig. 3.

APACHE CO.: Mt. Baldy, White Mountains, *Dahl & McGill M743* (ASU); *Pinkava et al. 11432A p.p.* and *11432B p.p.* (ASU); *Reeves 5271* (ASU).

COCONINO CO.: San Francisco Peaks: *Clausen & Trapido* (cited by Morton, 1951); *Little 4679* (cited by Maxon, 1942; Morton, 1951); Inner Basin, *Lehto et al. 16189 p.p.* (ASU); *Little 4740* (ARIZ, ASUF, MNA); *Romans 2* (ASU); *Romans & Hevly* (MNA); *Theroux, Keil & Reeves R5221* (ASU); *Hevly, Pinkava, Keil & Reeves R5308* (ASU); 0.3 km SW of Fremont Pass, along trail, associated with *Agropyron trachycaulum, Carex ebenea,* and *Festuca ovina,* 3277 m, *Reeves 5312* (ASU); Fremont Saddle, 3292 m, *Reeves 5328* (ASU).

5. B. boreale Milde. Northern Grape Fern. Fig. 7.

APACHE CO.: Mt. Baldy, White Mountains, *Reeves 5270* (ASU).

COCONINO CO.: San Francisco Peaks, Inner Basin, *Lehto et al. 16189 p.p.* (ASU); *Theroux, Keil & Reeves R5222* and *R5223* (ASU); *Hevly, Pinkava, Keil & Reeves R5306* and *R5311* (ASU); 0.3 km SW of Fremont Saddle, along trail, associated with *Agropyron trachycaulum, Carex ebenea,* and *Festuca ovina,* 3277 m, *Reeves 5313* (ASU); Fremont Saddle, 3292 m, *Reeves 5329* (ASU).

This is the most common *Botrychium* in Arizona. Considerable variation is found in the length of the stalk of the sterile blade, degree of dissection of the blade, and amount of overlap of the segments.

6. B. dusenii (Christ) Alst. Amphitropical Moonwort. Fig. 5.

APACHE CO.: Mt. Baldy, White Mountains, *Pinkava et al. 11432A p.p.* (ASU); *Reeves 5269* (ASU).

COCONINO CO.: San Francisco Peaks, Inner Basin, *Reeves 5310A* (ASU).

According to W. H. Wagner, Jr. (pers. comm.), the western plant usually identified as *B. minganense* Vict. or *B. lunaria* var. *onondagense* (Underw.) House is actually the southern hemisphere moonwort *B. dusenii,* which extends in North America from Los Angeles Co., California, to British Columbia and Alberta. The present report is the first record of it from Arizona. *Botrychium dusenii* differs

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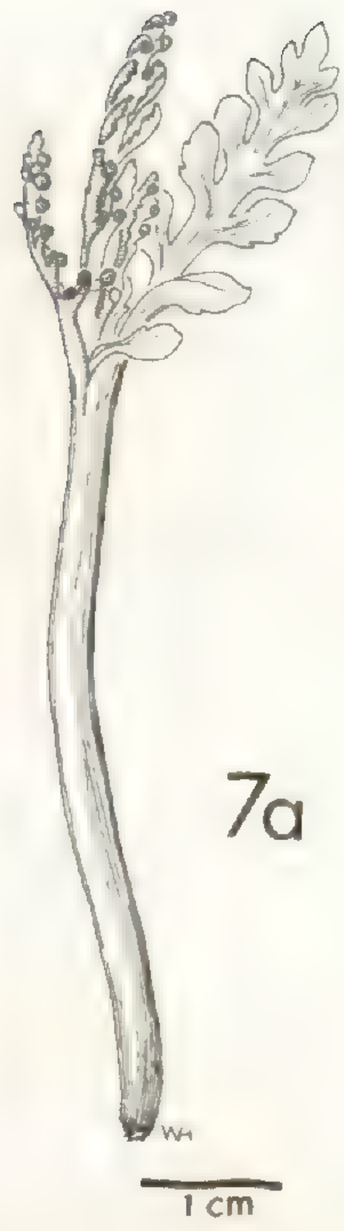
FIGS. 1-5. Plants of Botrychium. FIG. 1. *B. multifidum* var. *intermedium (Goodding & Schroeder, 340-41,* ASU). FIG. 2. *B. dissectum* f. *obliquum (Jackson,* ASU). FIG. 3. *B. lanceolatum* var. *lanceolatum (Lehto et al. 16189 p.p.,* ASU). FIG. 4. *B. lunaria* var. *lunaria (Pinkava et al. 11432A p.p.,* ASU). FIG. 5a. *B. dusenii (Pinkava et al. 11432A p.p.,* ASU). FIG. 5b. *B. dusenii (Reeves 5269,* ASU).



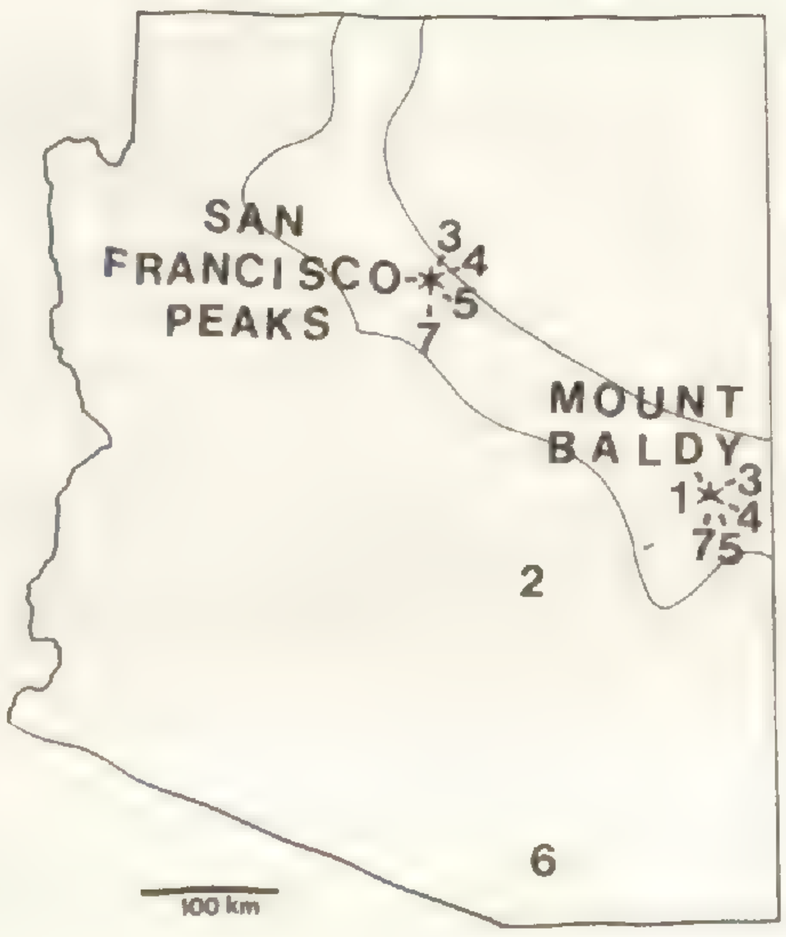


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FIG. 6. Plant of *Botrychium virginianum* (from photo of *Pringle*, ARIZ). FIG. 7a. *B. boreale* (*Lehto et al. 16189 p.p.*, ASU). FIG. 7b. *B. boreale* (*Reeves et al. 5306*, ASU). FIG. 8. Known distribution of botrychiums in Arizona. The numbers correspond to the illustrations. The outlined portion of the State is the Plateau section, based on Sellers and Hill (1974).

from *B. lunaria* in its narrower segments, which are commonly crenate along the distal margins and often more or less spatulate rather than flabellate. The segments are rarely overlapping, usually remote. Localities where *B. lunaria* occurs in the same habitat with *B. dusenii* are uncommon, but there are excellent examples in Washington. Evidently similar conditions prevail at the Arizona localities.

7. B. lunaria (L.) Swartz var. lunaria. Moonwort. **Fig. 4.**

APACHE CO.: Mt. Baldy, White Mountains, *Pinkava et al. 11432A p.p.* (ASU); *Reeves 5268* (ASU).

COCONINO CO.: San Francisco Peaks, *Collom 890* (cited by Maxon, 1942; Morton, 1951); Inner Basin, *Little 4741* (ARIZ, ASUF, MNA); *Theroux, Keil & Reeves R5220* (ASU); *Hevly, Pinkava, Keil & Reeves R5307* (ASU); Fremont Saddle, 3292 m, *Kearney & Peebles 12123* (ARIZ); *Reeves 5326* and *5327* (ASU); Agassiz Peak, SW-projecting slope of SW-projecting ridge on Agassiz Peak, *Johnsen* (MNA); *Schaack 379* (ASC); *Theroux, Keil & Reeves R5183, 5191, 5196,* and *5207* (ASU).

Most of the Arizona material of *B. lunaria* is referable to var. *lunaria*. There are a number of specimens that generally lack the flabellate divisions of var. *lunaria* and are usually smaller. The status of these specimens must await more detailed studies.

I wish to thank Dr. W. H. Wagner, Jr. for examining the specimens cited in this report. This research was supported in part by a grant from the Epsilon Tau Chapter (Arizona State University) of Beta Beta Beta Biological Society. I thank Ms. Elinor Lehto and Mr. Lyle McGill for providing locality data for botrychiums. I am especially grateful to the curators of Arizona herbaria for use of their facilities and the loan of specimens: Dr. C. T. Mason, Jr., ARIZ; Dr. J. M. Rominger, ASC; Ms. E. Lehto, ASU; Mr. C. P. Pase, ASUF; and Dr. W. B. McDougall, MNA. Drs. D. J. Pinkava and W. H. Wagner, Jr. have reviewed this paper and their critical comments and recommendations are greatly appreciated. Ms. Wendy Hodgson, a graduate student at Arizona State University, prepared the illustrations.

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New Taxa and Combinations of Ctenitis from Guatemala

ROBERT G. STOLZE*

Of all the genera I have studied in the preparation of "The Ferns and Fern Allies of Guatemala," *Ctenitis* has been one of the most troublesome. Despite Christensen's (1913, 1920) efforts to untangle the problems during his work on the comprehensive genus *Dryopteris*, the taxonomy remains quite confused. Collections are for the most part inadequate, as the difficulties encountered in the transportation and preparation of large ferns have prompted many botanists either to pass them by or to make only fragmentary specimens. Nevertheless, a new species has come to light, and I have also found it necessary to describe a new variety of *C. equestris*. In addition, two new combinations are needed for taxa occurring in Guatemala.

Ctenitis molinae Stolze, sp. nov. **Figs. 1–4.**

Plantae terrestres; rhizoma non visum; folia usque ad 1.5 m longa et 0.6 m lata, bipinnato-pinnatifida vel subtripinnata; petiolus rachisque muricata, paleis parce instructa; paleae usque ad 8 mm longae, rigidae, crassae, nitidae, margine integro et cellulis admodum elongatis; segmenta ultima oblonga vel subfalcata, integra vel crenata, glabra, minute glandulosa, margine eciliato; venae simplices vel 1-furcatae, terminantes ad vel prope marginem; indusium brunneum vel ochraceum, subpersistens, glanduloso-ciliatum.

TYPE: Slopes of Volcán Fuego, Depto. Chimaltenango, Guatemala, *Steyermark 52120* (US; isotype F).

Terrestrial, in wet forests, on slopes or on banks of streams or ravines, 1,200–1,800 m. Known from Guatemala, Honduras and Nicaragua.

Plants terrestrial, reported as acaulescent or as "tree ferns to 3 m tall," rhizome not seen; leaves evidently fasciculate, to 1.5 m long and 0.6 m broad; petiole to 0.7 m long, brown or yellowish, muricate with reddish, raised, persistent scale bases and provided with scattered, rigid, thick, lustrous, deep orange or castaneous scales, these to 8 mm long, commonly spreading, linear or linear-lanceolate, with margins entire and the cells greatly elongated and essentially conform (*i.e.* all similar in orientation, shape, size and color); lamina bipinnate-pinnatifid to subtripinnate, or rarely tripinnate-pinnatifid as to the bases of the lowest pinnae, firm-membranaceous, subdeltoid-ovate, the tissue commonly minutely glandular on both sides; rachis lustrous, muricate and scaly as on the petiole, terete abaxially, trisulcate adaxially, the grooves amply provided with unbranched, pluricellular, septate, reddish brown trichomes; pinnae slightly ascending, often subopposite, the lower ones short-stalked, scales of the axils few or lacking, scales of the costae abaxially like those of the rachis but much smaller and with the cells not so elongated, costae and costules adaxially provided with orange or reddish trichomes as on the rachis; ultimate segments oblong to subfalcate, entire to crenate, obtuse or subacute, glabrous except for a few, minute, articulated trichomes on the midrib adaxially, the margins eciliate; veins evident or somewhat obscure, simple, or once-forked in deeply crenate segments, terminating at or very near the margin; sori mostly inframedial on the veins; indusium dull brown or yellowish, subpersistent, glandular-ciliate.

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SELECTED SPECIMENS EXAMINED:

GUATEMALA: Quezaltenango: Above Mujuliá, between San Martin Chile Verde and Colomba, ca. 1,800 m. *Standley 85495* (F); western slopes of Volcán Zunil, opposite Santa María de Jesús, 1,500 m, *Steyermark 35102* (F, US). **HONDURAS: Morazán:** Montaña Uyuca entre Labranza and Granadillio, 1,800 m, *Molina 13584* (F). **NICARAGUA: Matagalpa:** Cordillera Central between Matagalpa and Jinotega, 1,300–1,500 m, *Williams, Molina & Williams 23529* (F).

This perhaps falls within Christensen's group of *Dryopteris ampla*, for in most characters it resembles species such as *Ctenitis equestris* (Kunze) Ching and *C. excelsa* (Desv.) Proctor. However, the scales of the axes are very distinctive. Those of the "*ampla*-group" are typically very abundant, and in places such as the rachis and pinna axils they may be so dense in some species as to nearly obscure the surface of the axis. They are usually thin-textured, relatively broad, acuminate or long-attenuate, and most of the cells are isodiametric or nearly so. The scales of *C. molinae* are scattered, and those of the primary axis *(Fig. 3)* are very rigid and thickened, linear, and not strongly tapered at apex. The cells are quite thick as seen in cross-section, often are thicker than broad, and most of them are very narrow and greatly elongated. The scale base is usually not expanded, but is quite firm and usually persistent, even when the rest of the scale has been broken off. Thus the rachis and petiole are often conspicuously reddish-muricate throughout. This kind of scale is not uncommon in the genus; similar rachis scales may be found for example in the Antillean *C. grisebachii* (Baker) Ching.

Other characters which are taxonomically important in *C. molinae* are the eciliate segment margins and the relatively large, subpersistent indusia *(Fig. 4)*. Most species in the "*ampla*-group" are exindusiate or have inconspicuous, fugacious indusia; and only *C. excelsa* has eciliate margins, the other species having the margins variously provided with minute, articulated trichomes.

Collections of *C. molinae* have been found in herbaria misidentified as *C. equestris* or as undetermined species of *Ctenitis*.

This species has been named in honor of Antonio Molina R. of the Escuela Agricola Panamericana, Tegucigalpa, Honduras, an indefatigable collector and one of the most competent of all Central American botanists. He has collected the new species in Honduras and Nicaragua, and throughout the years has provided many thousands of excellent specimens for the "Flora of Guatemala" project.

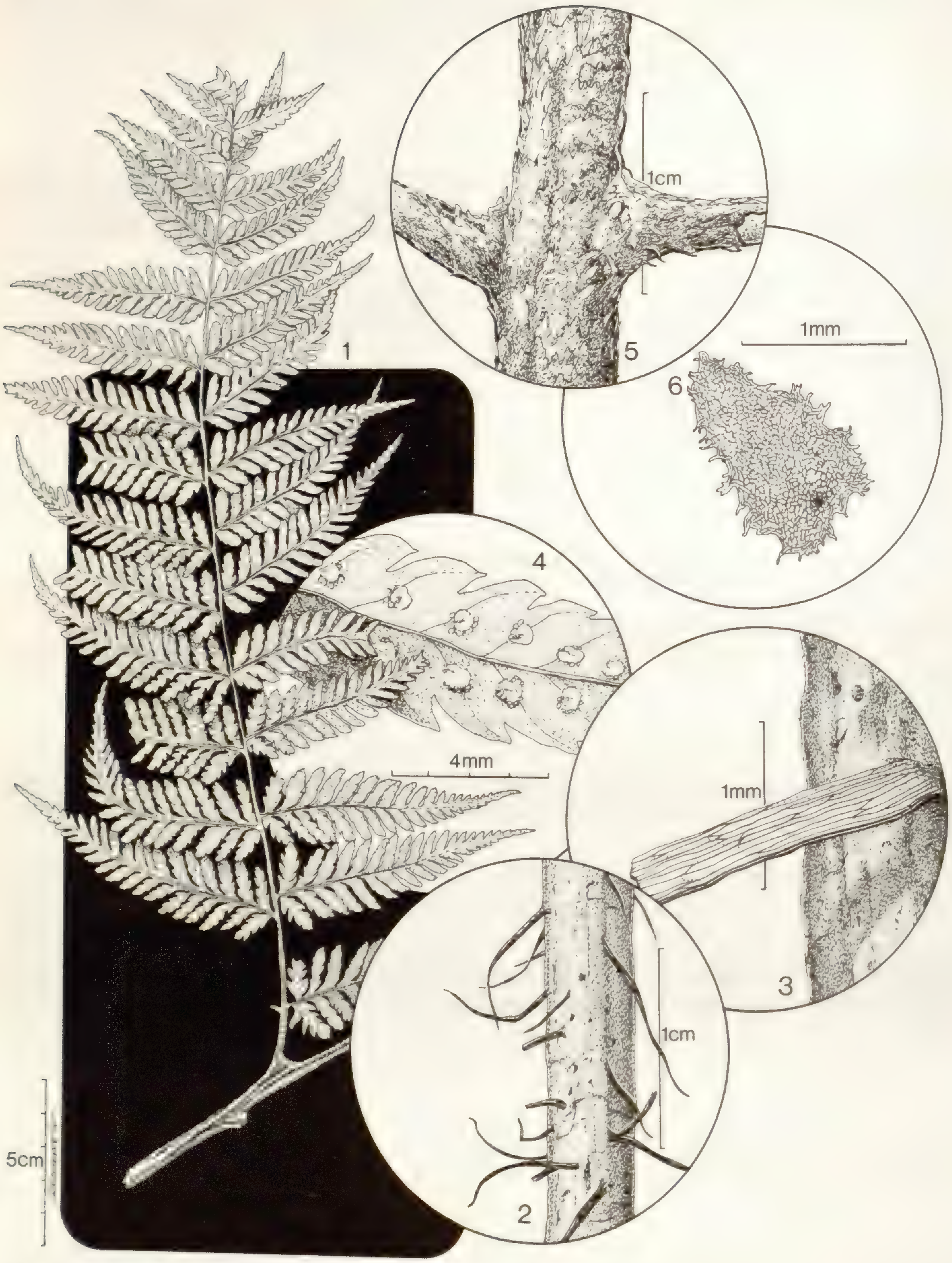
Ctenitis equestris (Kze.) Ching var. erosa Stolze, var. nov. **Figs. 5, 6.**

Paleae petioli superi necnon eae rachidis et axillarum pinnarum abundantes, saepe imbricatae et axem tegentes, aurantiacae, plerumque late ovatae, acutae vel acuminatae margine eroso et irregulariter denticulato vel breviter ciliato, pro parte maxima firme adpressae, cellulis plerumque isodiametricis; costularum paleae aurantiacae, flaccidae, complanatae; indusium nullum.

TYPE: Slopes of Cerro Tumbador, about 15 km west of San Marcos, Depto. San Marcos, Guatemala, *L. O. Williams et al. 23084* (F; isotype US).

Along banks of streams and in ravines, in deep forests, 2,400–2,700 m. Known only from Guatemala.

Scales of the upper petiole, rachis, and pinna axils abundant, often imbricate and fully concealing the axis, orange (sometimes reddish brown in center), commonly broad-ovate, acute to acuminate, the margins erose and irregularly denticulate or short-ciliate, mostly firmly appressed, the cells mostly isodiametric (some-



FIGS. 1-4. Holotype of *Ctenitis molinae*, *Steyermark 52120* (US). FIG. 1. Basal pinna. FIG. 2. Portion of petiole, with scales. FIG. 3. Portion of petiole scale, showing detail of cells. FIG. 4. Tertiary segment, with sori and persistent indusia. FIGS. 5-6. Holotype of *Ctenitis equestris* var. *erosa*, *Williams et al. 23084* (F). FIG. 5. Pinna axils, showing dense covering of scales. FIG. 6. Rachis scale.

times elongated toward scale apex); scales of the costules orange, flaccid, flattened; indusium lacking.

SELECTED SPECIMENS EXAMINED:

GUATEMALA: Chimaltenango; Ravine in oak woods, "Chichavac," about 8,100 ft, *Skutch 670* (US). **Quezaltenango:** Wet, brushy quebrada southeast of San Martin Chile Verde, ca 2,400 m, *Standley 83726* (F). **San Marcos:** Wet mountain forest near Aldea Fraternidad, between San Rafael Pié de la Cuesta and Palo Gordo, 1,800-2,400 m, *L. O. Williams et al. 26283* (F).

Ctenitis equestris var. *equestris* may be distinguished from the new variety by the following characteristics: scales of the rachis and upper petiole ample to scattered, commonly spreading and reddish brown or blackish, ovate-lanceolate to linear-lanceolate, attenuate, the margin subentire; scales of the pinna axils similar to those of the rachis, mostly blackish, the cells somewhat elongated (at the scale base sometimes isodiametric); scales of the costules reddish brown to blackish, rigid and spreading, commonly vaulted; indusium minute, light- or red-brown, glandular, very early fugacious.

Ctenitis equestris was included by Christensen (1920) in his "*Dryopteris ampla* group," a species complex as confused today as it was then. The entire group is badly in need of revision, and it is possible that many of the species within it are conspecific. Christensen's species concepts here were not altogether clear. For example, his key and descriptions point to "*D. ampla*" [=*C. sloanei* (Poepp.) Morton] as having ciliate segment margins, but a number of specimens he cited are obviously eciliate. The latter should have been included under *C. excelsa*, an eciliate species which Christensen described as being confined to a few Lesser Antillean islands. He also proposed for his *D. equestris* the two varieties *mentiens* and *heterolepis*. The former supposedly differed from the typical in the shape and remoteness of ultimate segments, characters which quite naturally vary with the relative size of the leaf. The latter is probably not *C. equestris* at all, but more likely *C. excelsa* (Desv.) Proctor.

It is unfortunate that another variety must be described in a species which is greatly misunderstood and perhaps very apt to be reduced to infraspecific status itself. However, in var. *erosa* the scales of the rachis and costae are the most distinctive in the entire species complex of *C. equestris-excelsa-sloanei*. Laminar scales throughout the complex are commonly slender (at most narrow-ovate), the margins essentially entire, and most of them spread somewhat from the axes. The laminar scales in var. *erosa (Fig. 6)* are often nearly as broad as long, the margins are erose and either irregularly denticulate or short-ciliate, and most of them are tightly appressed to the axes *(Fig. 5)*.

The following new combinations are needed for *Ctenitis* in Guatemala:

Ctenitis salvinii (Baker) Stolze, comb. nov.

Nephrodium salvinii Baker in Hook. & Bak. Syn. Fil. 274. 1867. TYPE: Guatemala, *Salvin & Godman s.n.* (K not seen).

Dryopteris salvinii (Baker) Kuntze, Rev. Gen. Pl. **2:** 813. 1891.

Ctenitis pulverulenta var. heydei (C.Chr.) Stolze, comb. nov.

Dryopteris karsteniana var. *heydei* C. Chr. Kongel. Danske Vidensk. Selsk. Skr., Naturv. Math. Afh. VIII, **6:** 77. 1920. TYPE: Río de los Esclavos, Depto. Santa Rosa, Guatemala, *Heyde & Lux s.n. (Donn.-Sm. 3249), pro parte* (US).

Some Heyde & Lux specimens bearing Donnel-Smith's distribution number 3249 represent a mixed collection. Four of these examined at the U. S. National Herbarium were all originally determined as *Nephrodium amplum* and each was stamped with a different herbarium number. Numbers 258590 and 830986 are isotypes of *Dryopteris karsteniana* var. *heydei,* but numbers 258596 and 830988 are *Ctenitis excelsa.*

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THE FERN GUIDE, **Northeastern United States**, by Dr. Edgar T. Wherry. Reprinted, paperback, 318 pages, illustrated, detailed, including culture of species. $3.00 postpaid. Quantity discount to dealers. MORRIS ARBORETUM, 9414 Meadowbrook Ave., Philadelphia, PA 19118.

The Lycopodium obscurum Complex in North America

R. JAMES HICKEY*

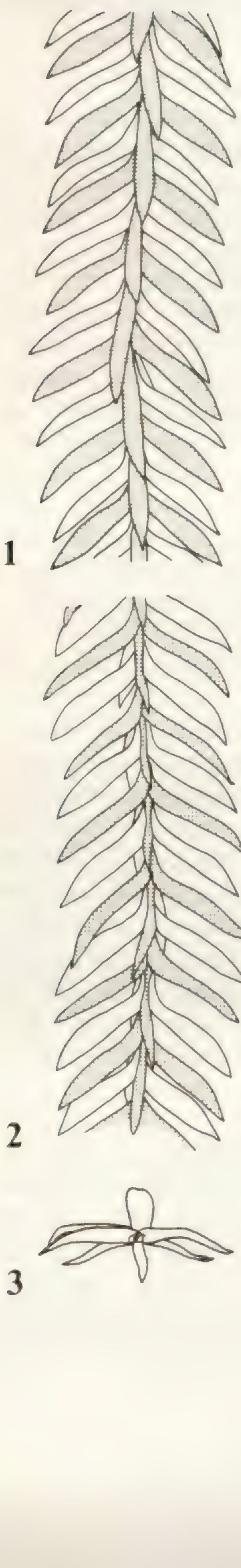
The taxonomic status and relationships of members of the *Lycopodium obscurum* complex have long been a problem for American taxonomists (Hauke, 1969). In the past, differentiation of the various taxa has been based on growth habit, the relative tereteness of the lateral branchlets when viewed end on, and on strobilus size and number. Unfortunately, no concerted effort has been made to examine the reliability of these characters or the morphological variation caused by the environment. Most taxonomists have concluded that these characters, and hence the taxa involved, show nearly complete intergradation. It is not surprising, therefore, that they have submerged *L. dendroideum* into *L. obscurum* or at best have recognized it as a form or variety of the latter. During a recent investigation (Hickey, in prep.) of the series *Obscura* (sensu Herter, 1950, p. 95), certain characters came to light which are stable under various ecological conditons and which show little intergradation of character states. These characters, when taken together, readily discriminate three North American taxa and do much to clear up the taxonomic difficulties which are present in this species complex. The purpose of this paper is to present these new characters, to redefine *L. dendroideum* and *L. obscurum* in light of them, and to describe as new *L. obscurum* var. *isophyllum*, which is endemic to eastern North America.

Variety *isophyllum* is common in the northeastern portion of its range and often assumes a fastigiate growth habit, thus mimicking *L. dendroideum*, for which it is most commonly mistaken. It is this mimicry, coupled with the occasional intergradation between *L. obscurum* var. *obscurum* and *L. obscurum* var. *isophyllum*, that is largely responsible for the belief that there is complete intergradation between *L. obscurum* and *L. dendroideum*. The general morphology and growth habit of all three taxa are so similar that in the individual descriptions mention will be made only of those characters where significant differences have been noted.

All of the taxa dealt with in this paper share the following characteristics: Subterranean rhizome clothed with sparse, broad and rounded, scale-like leaves; rhizome anisodichotomously branched with 1 upright leafy aerial shoot and 1 usually weak secondary rhizome produced each year; aerial shoots 8.0–19.0 (mean 12.5) cm from soil level to the base of the strobili, with 3 or 4 lateral branch systems along the aerial axis, each system dichotomously branched 3 or 4 times to produce 8–16 lateral branchlets.

Growth of the entire aerial shoot system is also similar in the three taxa. It continues for 4–5 years, and microphyll constrictions are present throughout the aerial portions. Dichotomous branching in the lateral branch systems is concentrated in the second growth season, with occasional dichotomies formed during the third growth season as well. Leaves of the lateral branchlets are normally 6-ranked and in two pseudowhorls of three leaves apiece, producing a phyllotactic fraction of 2/6. All leaves are strongly decurrent. Strobili, produced in the (sec-

*Gray Herbarium, Harvard University, 22 Divinity Ave., Cambridge, MA 02138.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ond) third and/or fourth growing season, are sessile or subsessile and terminal on either the main axis or on dominant branches of the lateral branch systems. For further information on the general growth habit of these plants see Primack (1973).

KEY TO THE LYCOPODIUM OBSCURUM COMPLEX IN NORTH AMERICA

1. Leaves of the lower portion of the main aerial axis diverging at angles of 30–90°; leaves of the lateral branchlets arranged in 2 dorsal, 2 ventral, and 2 lateral ranks (4 abaxial surfaces facing up and 2 abaxial surfaces facing down.....1. *L. dendroideum*
1. Leaves of the lower portion of the main aerial axis diverging at angles of less than 30°; leaves of the lateral branchlets arranged in 1 dorsal, 1 ventral, and 4 lateral ranks (3 abaxial surfaces facing up and 3 abaxial surfaces facing down).
   2. Leaves of all ranks equal in size and linear-attenuate; all leaves equally divergent from the branchlet axis; leaves of all ranks lying in planes tangential to the branchlet axis; angle of the leaf apex 21–36° (mean 27°).....2. *L. obscurum* var. *isophyllum*
   2. Leaves of the ventral rank smaller than those of the other ranks and linear-attenuate to long-triangular; leaves of the dorsal and lateral ranks linear-acuminate to linear-acute; dorsal and ventral leaves commonly appressed to the branchlet axis with only the lateral leaves strongly divergent; leaves of all ranks in parallel planes; angle of the leaf apex 27–59° (mean 40°).
      3. *L. obscurum* var. *obscurum*

1. Lycopodium dendroideum Michx. Fl. Bor. Amer. 2: 282. 1803. Figs. 7–9.

Lower portions of the aerial shoot with leaves strongly divergent (30–90°); leaves of the lateral branchlets in 2 dorsal, 2 ventral, and 2 lateral ranks; all leaves equally divergent from the lateral branchlets, the free leaf tips linear-attenuate, 2.35–5.45 (mean 3.9) mm long, 0.45–1.15 (mean 0.8) mm wide, with a leaf apex angle of 19–58° (mean 37°); lateral branchlets basically isophyllous but with a slight tendency toward reduction in size of the leaves of the lower ranks; strobili 1–14 (mean 2.4) per aerial shoot, 12.5–56.5 (mean 30) mm long.

LECTOTYPE: "in Carolina septentrionalis," *Michaux* (P seen on microfiche). Although the lectotypification of this taxon is discussed by Morton (1967, p. 180), he does not designate clearly which of the several plants is to be chosen the lectotype. To fix the application of this name, I choose the specimen in the upper left hand corner of the sheet as the lectotype.

DISTRIBUTION: Labrador, Newfoundland, Quebec, Prince Edward Island, New Brunswick, Maine, New Hampshire, Vermont, Massachusetts, New York, Pennsylvania, West Virginia, Ontario, Michigan, Wisconsin, Minnesota, Saskatchewan, Manitoba, Alberta, Montana, South Dakota, Washington, British Columbia, Yukon, Alaska, Asia.

2. L. obscurum L. var. isophyllum Hickey, var. nov. Figs. 4–6.

A *L. obscuro* var. *obscuro* foliis angustioribus, attenuatioribus, amplitudine aequalibus et ab axe aeque divergentibus differt.

Lower portion of the aerial shoot with leaves strongly appressed to slightly divergent (less than 30°); leaves of the lateral branchlets 6-ranked, with 4 lateral ranks, 1 dorsal, and 1 ventral rank; free leaf tips 2.5–5.0 (mean 4.0) mm long, 0.35–0.95 (mean 0.7) mm wide, linear-attenuate, straight to recurved, and all equally divergent from the axis of the lateral branchlet; leaf apex angle 21–36° (mean 27°). Strobili 1–10 (mean 3.4) per aerial shoot, 15.5–61.5 (mean 30.4) mm long.

FIGS. 1–3. *L. obscurum* var. *obscurum*. FIG. 1. Dorsal view of branchlet. FIG. 2. Ventral view of branchlet. FIG. 3. Distal view of branchlet. FIGS. 4–6. Same, *L. obscurum* var. *isophyllum*. FIGS. 7–9. Same, *L. dendroideum*. Shaded portions represent abaxial surfaces.

TYPE: Woods and marsh next to Powell Hollow, Rte. 322, 2 miles W of Cochranton, Crawford Co., Pennsylvania, July 5, 1974, *G. Williamson 91* (MU).

PARATYPES:

CANADA: Quebec: Quebec Co., Valcartier, bois abords du Camp, *Marie-Victorin 20802* (GH). **Nova Scotia:** Yarmouth Co., Belville, dry blueberry barren, *Fernald & Long 23090* (GH). **UNITED STATES: Massachusetts:** Hampden Co., Granville, *Seymour 129* (GH). **North Carolina:** Transylvania Co., near and on rocky summit of Devil's Courthouse, S of Sunburst (Lake Logan), elev. ca. 5750 ft, growing under *Kalmia, Hardin 709* (GH). **Ohio:** Portage Co., Windham Twp., dry open ground, *Webb 5594* (GH). **Wisconsin:** Adams Co., Dell Prairie Twp., sandy wooded slope at Witch's gulch, *Hartley 3370* (GH).

DISTRIBUTION: Nova Scotia, New Brunswick, Quebec, Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, New York, Pennsylvania, North Carolina, Michigan, Ohio, Kentucky, Tennessee, Wisconsin, Minnesota, Indiana.

3. L. obscurum L. var. obscurum, Sp. Pl. 2:1102. 1753. Figs. 1–3.

Leaf divergence in the lower portions of the aerial stems and leaf ranks of the lateral branchlets as in var. *isophyllum;* dorsal and lateral leaves linear-acuminate to linear-acute; leaves of the ventral rank much smaller than those of the other ranks and linear-attenuate to long-triangular; lateral leaves twisted so as to lie parallel with the leaves of the dorsal and ventral ranks; leaves of the lower lateral rank smaller than those of the upper lateral rank and often recurved toward the branchlet axis; leaves of the dorsal and ventral ranks commonly appressed to the branchlet axis, giving, together with the small leaves of the lower rank, the plant having a heterophyllous appearance; leaves 1.25–6.25 (mean 3.6) mm long, 0.35–1.15 (mean 0.8) mm wide, with a leaf apex angle of 27–59° (mean 40°). Strobili 1–10 (23) (mean 2.9) per aerial shoot, 11.5–59.5 (78.5) (mean 34) mm long.

LECTOTYPE: To fix the application of this name, I choose plate LXVII of Dillenius' "Historia Muscorum," as published in 1741. Since it is obvious that the plate was reengraved for later editions and that it is this publication that Linnaeus was referring to in his description, only this plate, which depicts a sterile specimen, should be regarded as the lectotype. Linnaeus' specimen (LINN 1257.12, seen on microfiche) is immature, not identifiable to variety or perhaps even species, and not a suitable lectotype.

DISTRIBUTION: Nova Scotia, Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, New York, Pennsylvania, New Jersey, Maryland, Delaware, Virginia, North Carolina, Alabama, Michigan, Ohio, Kentucky, Tennessee.

My thanks are extended to Dr. W. H. Wagner, Jr., Dr. Rolla Tryon, Melissa Bristol, and Ray Umber for their help during this study, with my special thanks extended to Wendy McNeill and Dr. Hardy Eshbaugh for their continued encouragement and support.

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A Chromosome Count and Range Extension for Christensenia (Marattiaceae)

A. F. BRAITHWAITE*

Of the six genera recognised by Copeland (1947, pp. 14-17) in the Marattiaceae, there are cytological records in the literature for *Angiopteris*, *Marattia* and *Danaea*. These numbers are: $n = 40$ (Manton & Sledge, 1954; Mehra & Singh, 1955) and $n = 80$ (Manton & Sledge, 1954; Ninan, 1956) for *Angiopteris*; $n = 39$ (Brownlie, 1961), $n = 78$ (Ninan, 1956), and $n = 40$ (Walker, in Manton, 1959; Walker, 1966) for *Marattia;* and $n = 80$ and triploid hybrids showing 40 bivalents and 40 univalents for *Danaea* (Walker, 1966). These chromosome counts show that *Angiopteris* and *Danaea* have a base number of 40, whereas *Marattia* has two base numbers, 39 and 40, the lower number being derived by the loss of one chromosome (Walker, 1966). The cytological uniformity of the representatives which have been examined so far underlines the distinctive morphological, anatomical and embryological characteristics shared by the genera (Campbell, 1911; Bower, 1926). No cytological information is available for two of the remaining genera, *Archangiopteris*, *Macroglossum*, or, until now, for *Christensenia*.

Christensenia is unique in the Marattiaceae in possessing palmately divided fronds with scattered, round synangia and reticulate venation. It is found in Assam, Malaysia, Sumatra, Java, Bali, Borneo, and the Philippines. Throughout its range several species have been described, but these are doubtfully distinct and, pending critical taxonomic investigation, all the variants are perhaps best regarded as forms of one species, *C. aesculifolia* (Blume) Maxon. The genus has not been reported previously from the Solomon Islands, but in the 1960's it was found by different collectors on three of the major islands.

During the 1965 Royal Society Expedition to the British Solomon Islands, *C. aesculifolia* was found by the author on San Cristobal, the southeasternmost island, growing in the lowland forest approximately seven miles inland from Wainoni Bay near the confluence of the Warahito and Pagato Rivers. It was evidently very localized, since considerable searching in the area revealed only two small populations in deep shade on the steep banks of two small calcareous streams feeding the Pagato and Sumaro Rivers respectively (*RSS 4215*, 28 July 1965, K; *RSS 4220*, 29 July 1965, K). In addition, specimens are known from the Buin area, Bougainville (25 July 1964, *Schodde 3674,* CANB) and from Allardyce Harbour, Santa Ysabel (4 Feb 1967, *BSIP 8271,* HON, K). These records represent a notable extension of the range of the genus eastwards into Melanesia and place *Christensenia* in a small group of Malesian fern genera now known to reach their southern limit in the Solomon Islands. It is of some phytogeographical interest to note that, so far as the author is aware, the genus has not yet been found in New Guinea, although this may merely be a reflection of insufficient botanical exploration.

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The field-fixed material from San Cristobal (*RSS 4220*) yielded several cells at diakinesis and metaphase I of meiosis which gave chromosome counts of $n = 80$ (*Fig. 1*) and one spore mother cell undergoing anaphase separation which gave $2n = 160$.

The count of n = 80 for *Christensenia* agrees with the chromosome numbers already reported in the literature for other genera in the Marattiaceae. Since diploids with $n = 40$ are known in *Angiopteris* and *Marattia* and tetraploids with $n = 80$ are recorded in *Angiopteris* and *Danaea*, it seems reasonable to suggest that *C. aesculifolia* from the Solomon Islands is also a tetraploid species based on $x = 40$. Thus the cytological evidence confirms the naturalness of the family and substantiates the phylogenetic implication of a common ancestry of the genera.

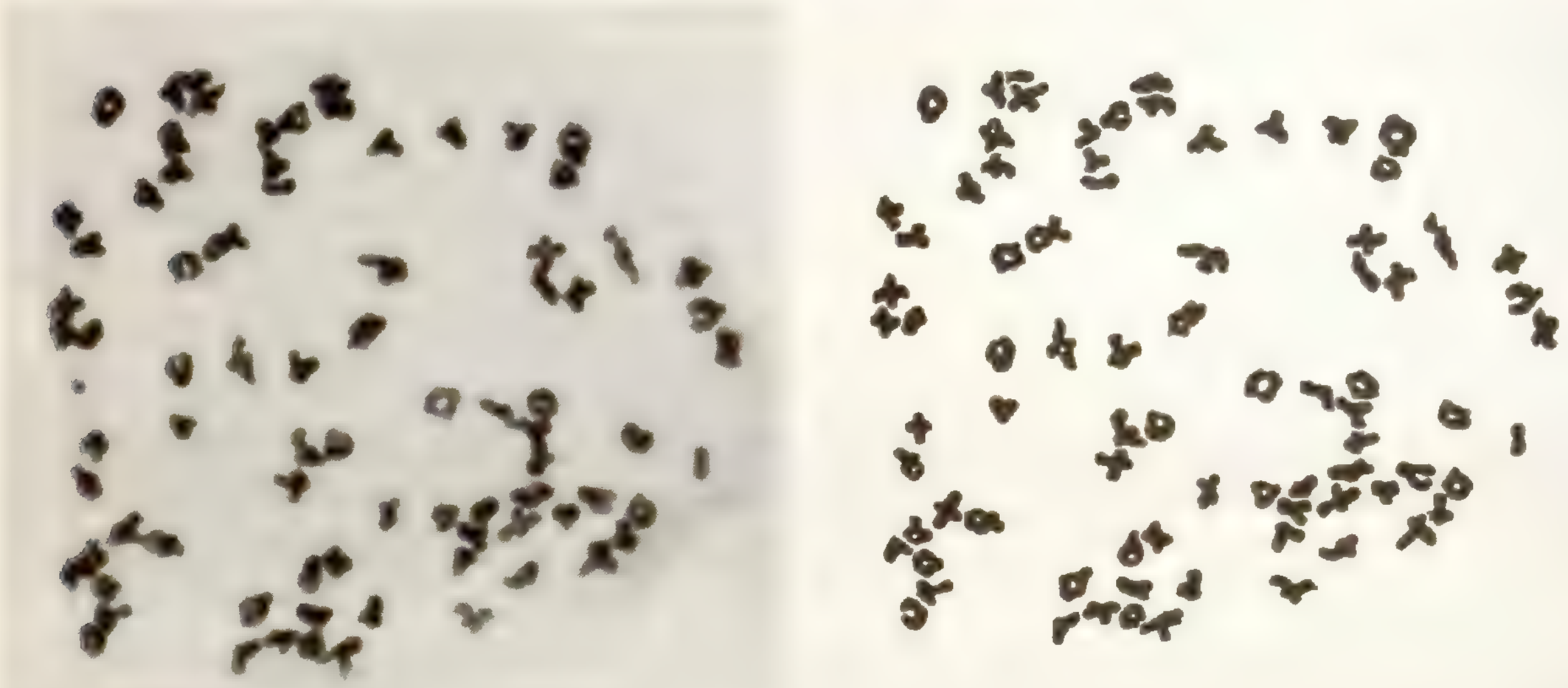

FIG.1. Acetocarmine squash preparation of meiosis in *Christensenia aesculifolia* (Blume) Maxon from the Solomon Islands (*RSS 4220*) with 80 bivalents, × 1000, with interpretive drawing at right.

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The Discovery of Athyrium filix-femina and Other Interesting Pteridophytes in Southeastern Kansas

RALPH E. BROOKS and JANET B. ROTH*

The Lady Fern, *Athyrium filix-femina* (L.) Roth, is included in the Kansas flora in several early publications (Wilson, 1875; Gates, 1940). Apparently its inclusion was based on cultivated specimens, as is discussed in detail by McGregor and Hartman (1956). Recent floristic work excludes the species from Kansas (McGregor, Brooks & Hauser, 1976).

FIG. 1. Looking down a wooded ravine along sandrock outcroppings, a typical scene in the Chautauqua Hills.

In August, 1976, the junior author and a field team of biologists from the State Biological Survey of Kansas discovered a lush, wooded ravine in south central Chautauqua County near the Oklahoma state line (*Fig. 1*). The area is part of the Chautauqua Hills and represents the northern limits of the Texas Biotic Province. The Chautauqua Hills are characterized by low, rolling hills capped with sandstone and covered primarily with Post Oak (*Quercus stellata*) and Blackjack Oak (*Q. marilandica*), which form an oak savannah. Calcareous rocks are some-

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times exposed from water erosion in deep ravines in the area. A representative collection of the pteridophytes of the area was made, and it was later discovered that in the collection was a plant of *Athyrium filix-femina* subsp. *asplenioides* (Michx.) Hultén, following Liew (1972) and Lellinger (1975).

The senior author visited the locality in October, 1976, and discovered a thriving population of approximately 75 plants. The tremendous mass of rhizomes observed suggests that these plants have been in existence for many years. The lady ferns were restricted to an area below a sandrock ledge in a small ravine. Heavy seepage in this area causes the sandy ground to remain wet and forms a small stream that soon joins a larger stream in the valley below. Specimen data are as follows: Chautauqua County, 0.75 mi. S and 1.5 mi. E of Chautauqua, 18 Aug 1976, *J. & S. Roth 166; R. E. Brooks 12824* (KANU).

In addition to the Lady Fern, the ravines in the immediate area provide suitable habitats for a variety of other ferns and fern allies. Most notable is *Osmunda regalis*, a species previously known in Kansas from a single extant station in Wilson County. It was found in abundance with two other ferns, *Thelypteris palustris* and *Onoclea sensibilis*, in the wet, sandy ravine at the Chautauqua County locality. Interestingly, numerous individual plants of *Onoclea* were observed with fronds varying from sterile to half sterile and half fertile to fully fertile. Likewise, plants bearing typical sterile and fertile fronds produced fronds with pinnatifid pinnae or pinnae with both fertile and sterile segments. Such variation certainly indicates that the epithet *obtusilobata* should be relegated to synonomy under *Onoclea sensibilis*, as was done by Lloyd (1971).

On north-facing sandrock ledges and walls were found *Asplenium platyneuron, A. trichomanes, Cystopteris tennesseensis, Dryopteris marginalis*, and *Woodsia obtusa*. Blanketing moist loam banks above the stream was *Cystopteris protrusa* and an occasional rare specimen of *Polystichum acrostichoides*. Dryer ledges with southern exposures harbored individuals of *Cheilanthes lanosa* and occasional mats of *Selaginella rupestris*.

The discovery of the Lady Fern in this locality extends the range 120 miles westward from western Missouri. It seems likely that the species should occur in nearby southern areas of the Texas Biotic Province, but the nearest stations in Oklahoma are about 290 miles southeast of the Chautauqua County locality. Perhaps additional field studies will reveal the presence of the Lady Fern in the intervening area.

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Two Unusual Features in Thelypteroid Ferns and Their Evolutionary Significance

D. S. LOYAL*

This paper concerns the multiple-stranded leaf traces of *Pronephrium lakhimpurense* (Rosenst.) Holtt. (syn. *Thelypteris rubra* (Ching) Iwats. or *Abacopteris rubra* (Ching) Ching) and the often peltate rhizome scales of *Ampelopteris prolifera* (Retz.) Copel. (syn. *Thelypteris prolifera* (Retz.) Reed). Since both of these features are contrary to what have been regarded as diagnostic characters for the Thelypteridaceae, their evolution and possible phylogenetic significance are discussed.

Material of *Pronephrium lakhimpurense* was collected in the eastern Himalayas. This fern is fairly common in Sikkim and the Darjeeling Himalayas; it grows on humus-rich, wet soils, especially near water courses, at 300-600 m elevation. *Ampelopteris prolifera* was collected on the Punjab plains. Leaf traces were studied from sectioned material, as well as from rhizome segments cleared in Schultz's macerating fluid. Scales were prepared for camera lucida drawings by clearing them in aqueous sodium hydroxide.

OBSERVATIONS

Multiple-stranded leaf traces in Pronephrium lakhimpurense.—The rhizome is short and somewhat ascending, with closely set fronds 2 m or more long and 60 cm wide. The rhizome contains copious, red mucilage to which the specific epithet *rubra* refers. The vascular system is a radially symmetrical dictyostele comprising 3 or 4 meristeles (*Fig 1*). The leaf trace is composed of four major strands, unlike the binary condition observed in the allied species *T. multilineata* (Wall. ex Hook.) Morton (syn. *A. multilineata* (Wall. ex Hook.) Ching) and the thelypteroid ferns in general. Of these strands, the two lateral ones are flattened (*Fig. 2*). They depart from the axial stele enclosing the gap well above the middle of the gap (*Fig. 3*, L st). Thus in position and outline in cross-section, they are homologous to the strands in other thelypteroid ferns, the only notable difference being the basal perforation resulting from the parenchymatization of the vascular strand slightly above the point of the strand's divergence from the axial stele. No other thelypteroid fern thus far known shows this feature. In addition, the abaxial part of the leaf base is traversed by two major strands which depart from the proximal part of the leaf gap (*Fig. 3*, Ab st). These strands are circular in cross-section and are smaller than the lateral strands. All four strands are connected by a few additional, smaller strands in the rhizome or in the proximal part of the stipe; the fusion of these strands begins in the distal part of the stipe and is completed in the rachis.

Rhizome scale ontogeny and attachment in Ampelopteris prolifera.—Holttum (1954, p. 299) observed a few peltate scales on the abaxial side of the costae in this

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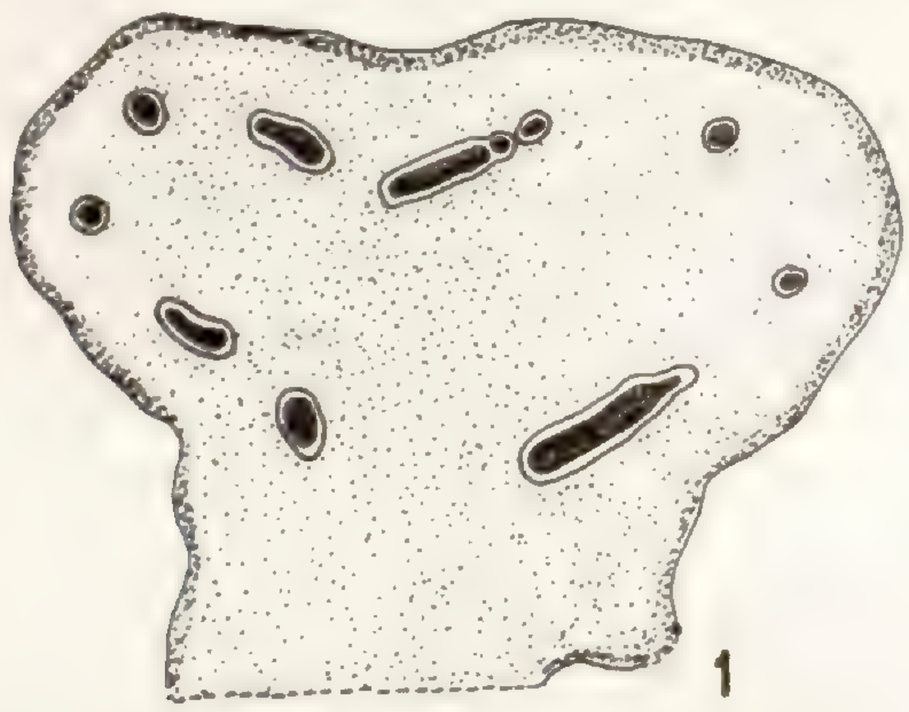
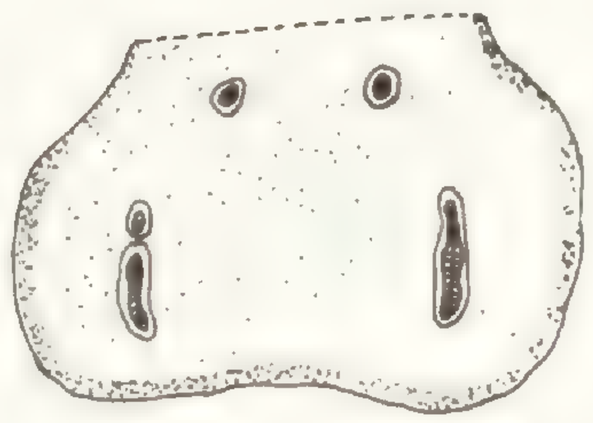
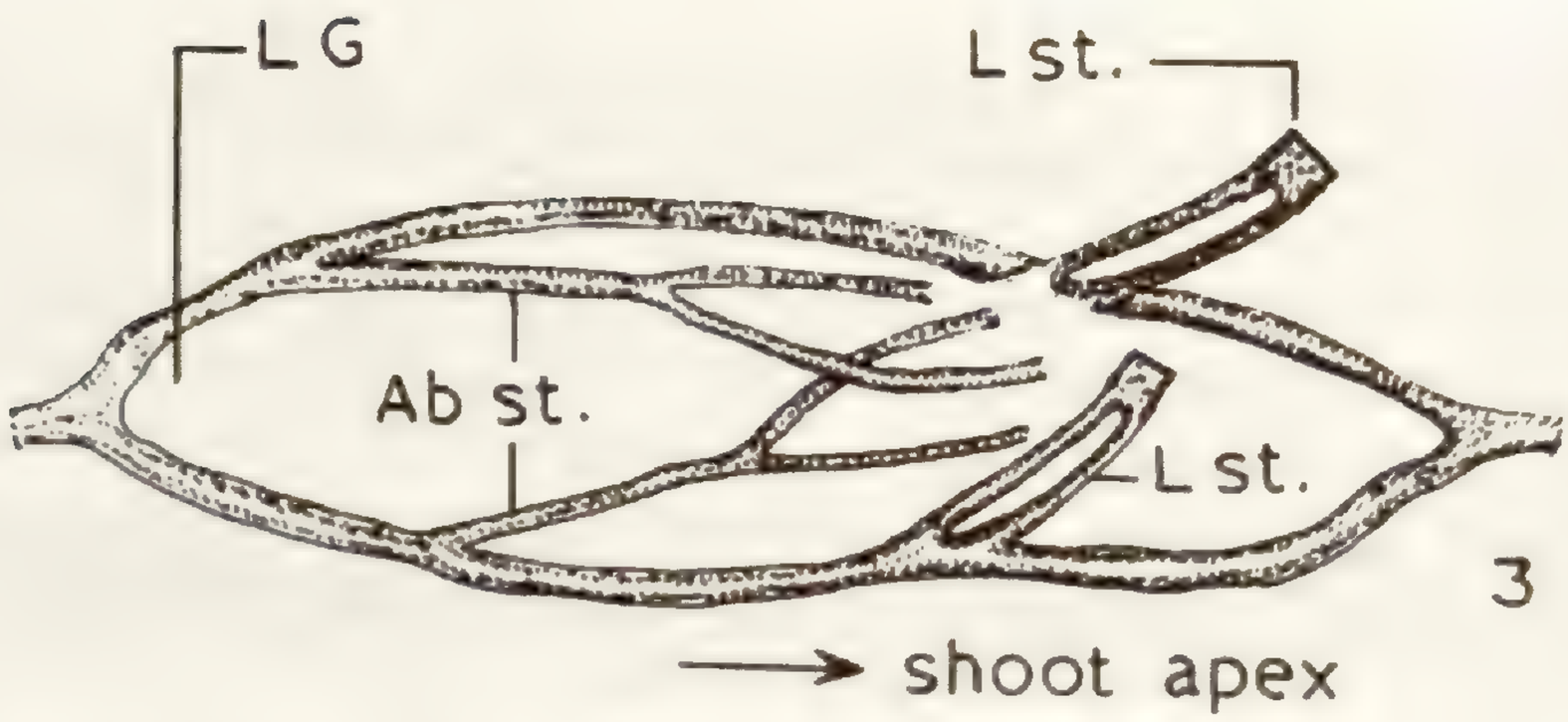
species. Iwatsuki (1962, p. 103), however, remarked that Holttum's "observations may be a misunderstanding of the structure of the basifixed scales. Really, the bases of them are very deeply cordate with imbricate lobes." Chandra and Nayar (1968) described the rhizome scales as being all pseudopeltate. Holttum et al. (1970) described the ontogeny of the rhizome scales, but not the variation in attachment and structure of the mature scales. A detailed study of these scales was made in order to resolve this controversy. Only shoot apices were examined because the scales soon fall off, leaving the older rhizome surface practically naked.



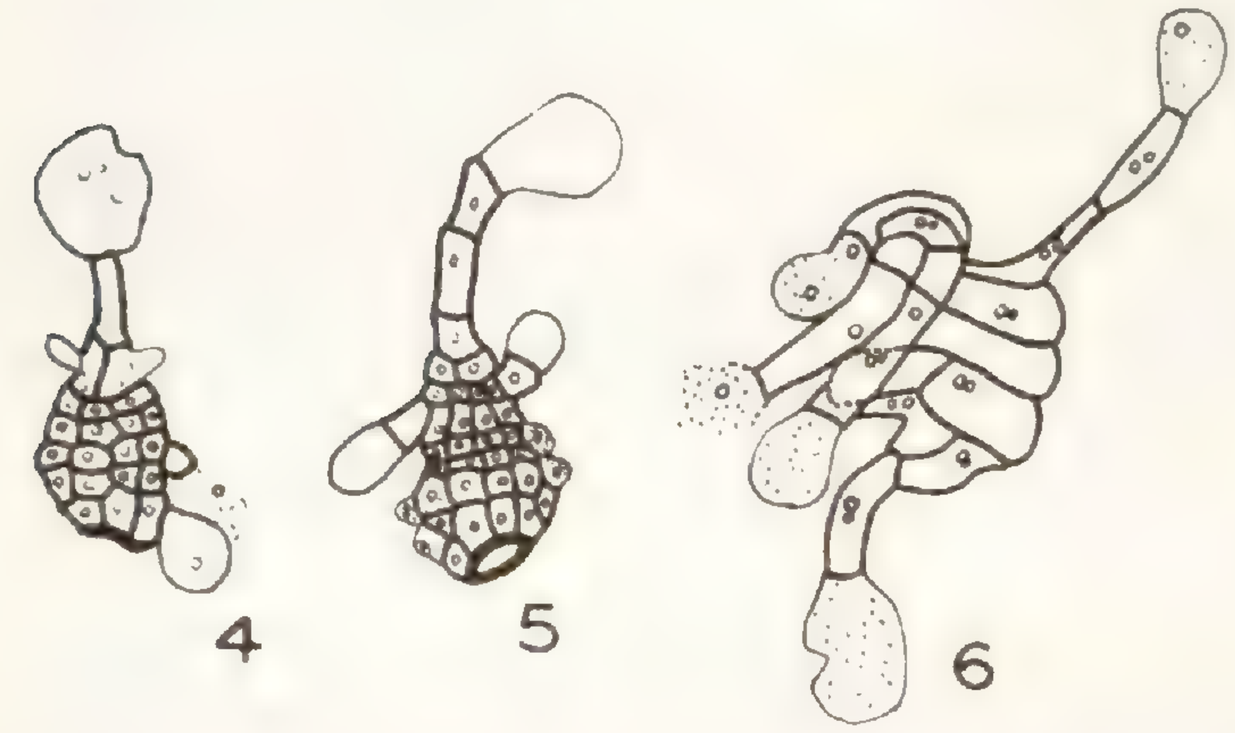


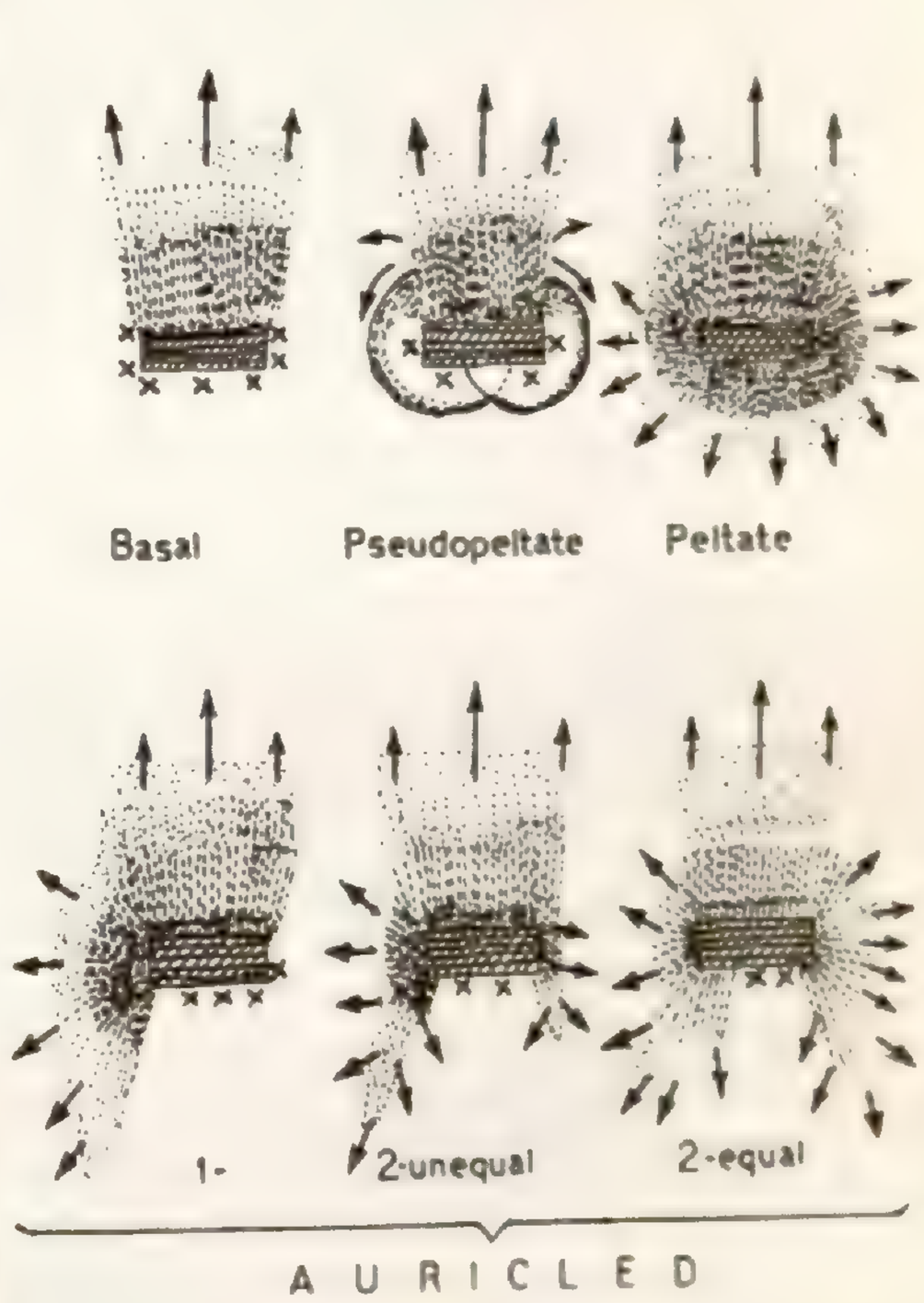


Rhizome and frond vasculature of *Pronephrium lakhimpurense*. FIG. 1. Transection of portion of rhizome, × 4.5. FIG. 2. Transection of portion of proximal part of the petiole, × 4.5. FIG. 3. Diagrammatic sketch of a single leaf gap and leaf trace. L st = Lateral strand, Ab st = Abaxial strand, LG = Leaf gap.

The apical dome and the overlying leaf buttresses are covered by the youngest, juvenile scales, which have predominantly basal attachment (*Figs. 4-6, 8-10*); those with peltate attachment (*Fig. 7*) were extremely rare in this region. The scales' club-shaped terminal cell and a number of marginal cells were glandular at various stages of development, and the appearance of 1-4 nucleolar-like bodies marked the culmination of their growth.

In the subdistal part of the shoot apex, the juvenile scales complete their growth both by cell division and cell expansion. A critical analysis of their growth patterns, as schematically represented in *Fig. 11*, revealed four different modes of attachment: basal (*Figs. 12, 18, 19* and *22*), lateral (*Fig. 17*), pseudopeltate with imbricate lobes and auricled (*Figs. 14, 15,* and *23*), and peltate (*Figs. 13, 20, 21,* and *24*). The variation in shape at maturity was even greater than the variation in mode of attachment and, indeed, defied precise categorization. Both mode of attachment and shape of the mature scales can be attributed to variation in space





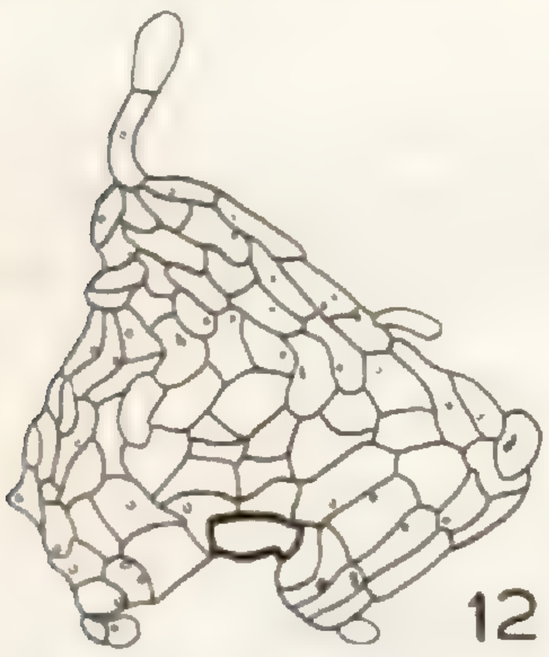
Scales of *Ampelopteris prolifera*. FIGS. 4-10. Juvenile scales from the rhizome apex, × 50. Heavily outlined areas = point of attachment. FIG. 11. Schematic representation of scale attachment in the subdistal part of the rhizome apex. Cross-hatched area = point of attachment, ×'s = absence of meristematic activity, arrows = direction of growth.

and time of cell divisions. Differences in space determine the mode of attachment and shape of mature scales, especially in their basal region. Differences in time cause scales of different developmental stages (juvenile, intermediate, and mature) to be intermixed in the subdistal part of the rhizome apex.

DISCUSSION

According to published reports, binary leaf traces occur uniformly in Old World species of Thelypteridaceae. This character has rightly served as one of the reliable diagnostic characters of the family (Holttum, 1947, 1973, p. 174; Loyal, 1963; Iwatsuki, 1963, p. 31). The occurrence of multiple-stranded leaf traces in *P.*

lakhimpurense involves problems of evolutionary and morphogenetic interpretation. In view of the striking similarity of the two lateral strands with those of other members of the family, especialy the allied species *T. multilineata*, it seems to me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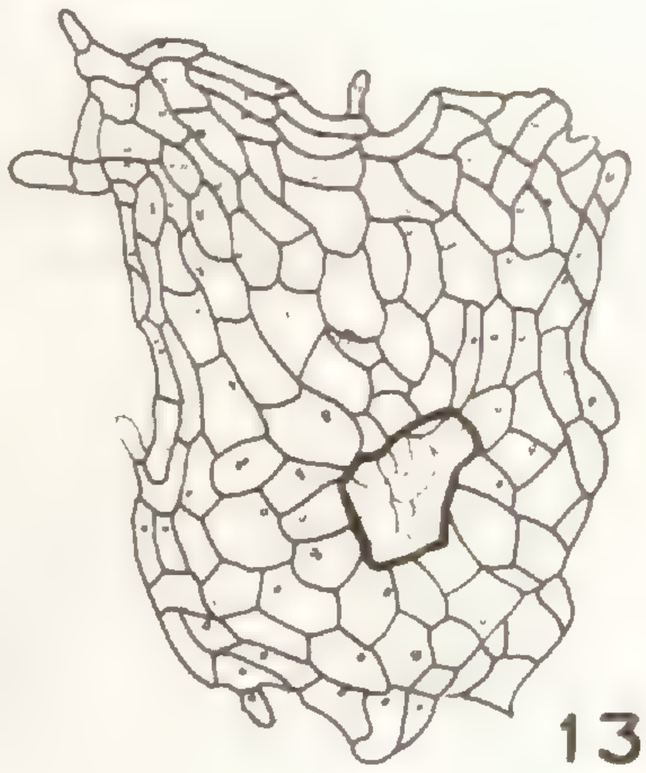
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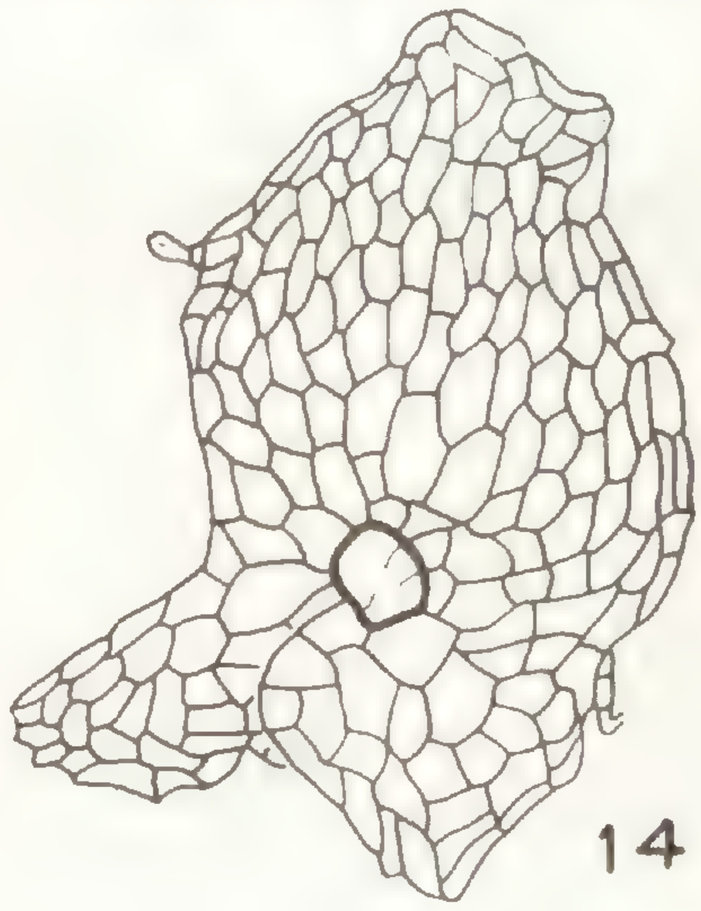
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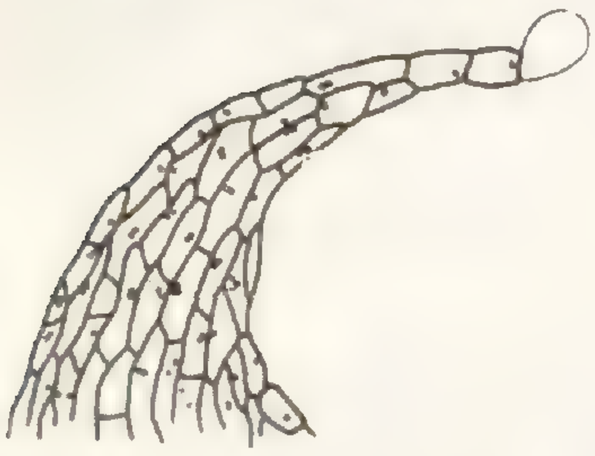

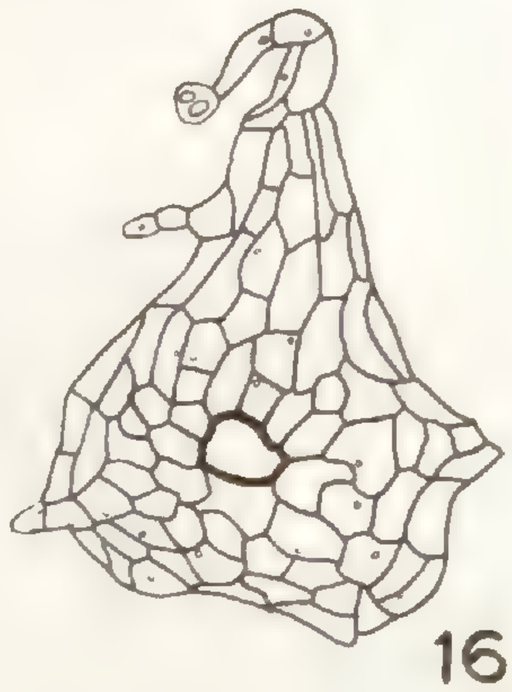
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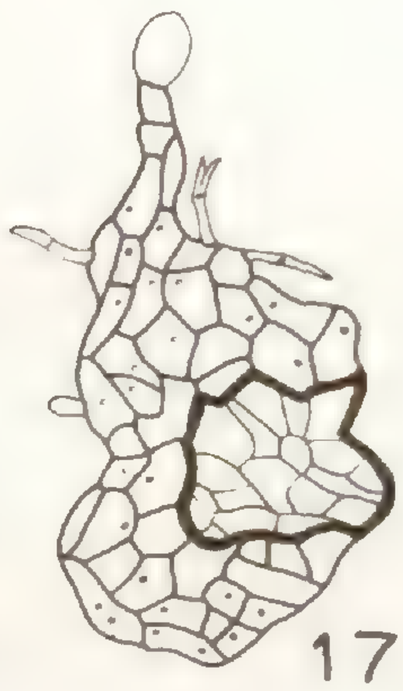
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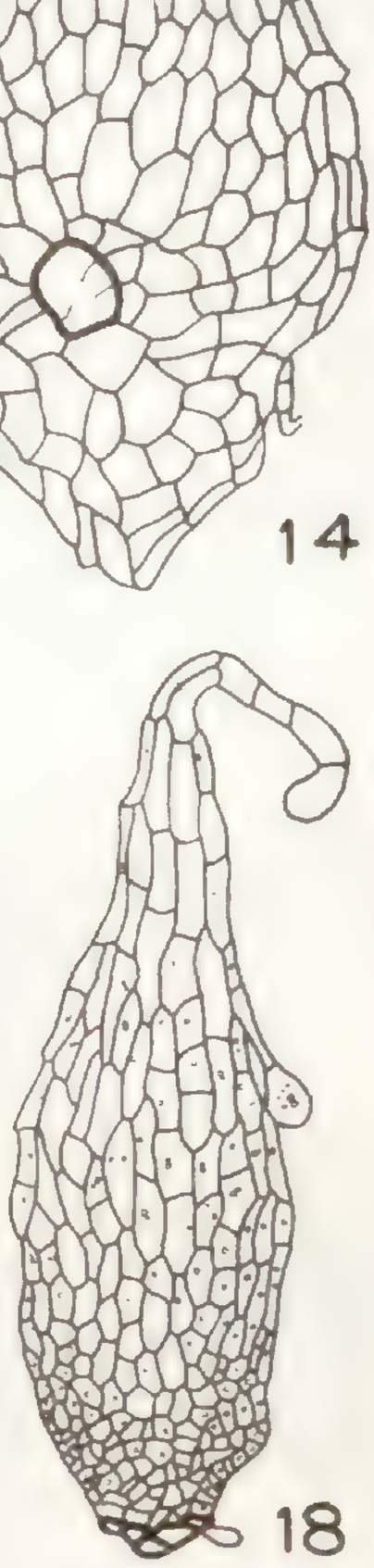
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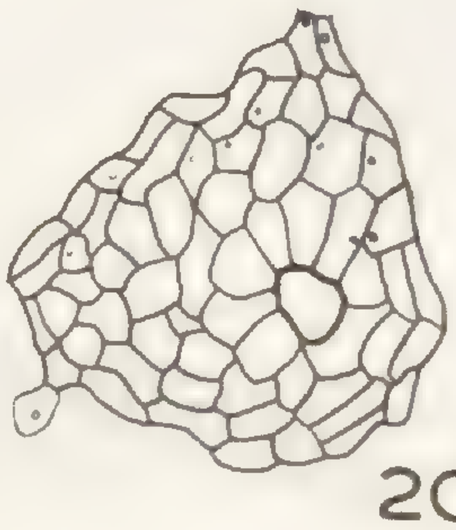
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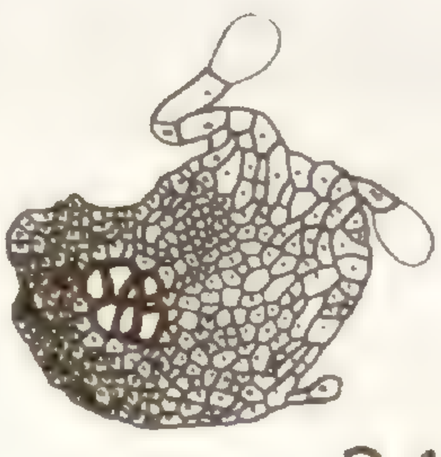
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Scales of *Ampelopteris prolifera*. FIGS. 12-24. Variation in attachment and structure of adult scales in subdistal part of the rhizome apex, × 53.

certain that two lateral strands represent the original evolutionary state and that the abaxial strands are doubtless accessory and an advanced condition. An analogy can be found in the eastern Himalayan *Diplazium latifolium* (another species which is larger than most in its genus), which has 4–7 petiolar strands, in contrast

to the usual binary condition in other species of the genus (Bir, 1969). In both the *Pronephrium* and the *Diplazium*, the multiple-stranded leaf trace has evolved independently. I believe this does not imply phylogenetic relationship with ferns having similar leaf traces, like the cyatheoid and dryopteroid ferns, for instance. From a morphogenetic standpoint, the parenchymatization in the basal region of the two lateral strands is very interesting, since its differentiation probably is influenced by the same set of factors that operate during leaf gap formation in the rhizome vascular system, a phenomenon which Wardlaw (1968, p. 144) has called parenchymatization. This developmental aspect obviously needs further study.

Two important points emerge from the study of *Ampelopteris prolifera* rhizome scales. First, Holttum's earlier report of the occurrence of peltate scales in this fern is confirmed, although they are less abundant than those of other types. Second, the usual rigid genetic control of development leading to uniform scales having only one kind of attachment does not seem to apply.

Interestingly, in contrast to bilateral spore symmetry generally known in Thelypteroid ferns, *Macrothelypteris torresiana* (Gaud.) Ching (syn. *Thelypteris torresiana* (Gaud.) Alston) and *Lastrea tenericaulis* (Hooker) Moore have tetrahedral spores (Chandra, 1973). This unusual feature also represents evolutionary innovation in the family and is still another example of parallel and convergent evolution in ferns.

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Nomenclatural Notes on Some Ferns of Costa Rica, Panama, and Colombia

DAVID B. LELLINGER*

My studies of tropical American ferns have led to the recognition of some new species of ferns that have been (Proc. Biol. Soc. Washington **89:** 703–732. 1977) or will be published elsewhere. Others already have epithets, but not in the correct genera as I understand them. For these, the following new combinations are proposed. A few names above the specific level are included.

Arachniodes denticulata var. barbensis (C. Chr.) Lellinger, comb. nov.

Dryopteris denticulata var. *barbensis* C. Chr. K. Danske Vidensk. Selsk. Skr., Natur. Math. Afd. VIII, **6:** 115. 1920. LECTOTYPE: In order to fix the application of this name, I choose: Volcán Barba, Pcia. Heredia, Costa Rica, *Pittier 1932* (US; isolectotypes B not seen, P not seen). The other syntype is: Volcán Barba, *Hoffmann 79* (B not seen).

This variety apparently has evolved locally from var. *jucunda* in the high mountains of southern Mexico, Guatemala, Costa Rica, and Panama. It is larger and more divided than var. *jucunda*.

Arachniodes denticulata var. jucunda (Fée) Lellinger, comb. nov.

Aspidium jucundum Fée, Icon. Esp. Nouv. 41. 1865. LECTOTYPE: Edo. Oaxaca, Mexico, 7500 ft alt, *Galeotti 6563* (P or RB not seen; isolectotype BR not seen photo 5181), chosen by Christensen (K. Danske Vidensk. Selsk. Skr., Natur. Math. Afd. VIII, **6:** 120. 1920). The other syntype is: Cuba, *Linden 2115* (P not seen photo 4675; isosyntypes BM not seen photo 6409, BR not seen Weatherby photo), and is *Arachniodes formosa* (Fée) Ching.

Blotiella lindeniana var. decomposita (Christ) Lellinger, comb. nov.

Lonchitis lindeniana var. decomposita Christ, Bull. Herb. Boiss. II, **6:** 190. 1906. TYPE: Valley of the Río Navarro, Pcia. Cartago, Costa Rica, 1400 m alt, *Wercklé* (P not seen; isotype US).

Campyloneurum heterolepis (Rosenst.) Lellinger, comb. nov.

Polypodium angustifolium var. *heterolepis* Rosenst. Mém. Soc. Neuchatel Sci. Nat. **5:** 54, *f. 7.* 1912. TYPE: Forests around the cafetal La Camelia near Angelopolis, Depto. Antioquia, Colombia, ca. 1800 m alt, *Mayor 140* (P not seen; isotype UC).

This species differs from *C. angustifolium* (Swartz) Fée in having large, non-clathrate, narrowly lanceolate, entirely stramineous rhizome scales. It is known from Venezuela, Colombia, and Ecuador.

Ctenitis chiriquiana (C. Chr.) Lellinger, comb. nov.

Dryopteris chiriquiana C. Chr. K. Danske Vidensk. Selsk Skr., Natur. Math. Afd. VIII, **6:** 36. 1920. TYPE: Upper Caldera River, Holcomb's trail above Boquete, Pcia. Chiriquí, Panama, 1450–1650 m alt, *Maxon 5729* (US).

Ctenitis melanosticta var. bullata (Christ) Lellinger, comb. nov.

Aspidium bullatum Christ, Bull. Herb. Boiss. II, **6:** 53. 1906. TYPE: Navarro, Pcia. Cartago, Costa Rica, 1400 m alt, *Wercklé* (P not seen; isotype US).

Diplazium atirrense (Donn. Sm.) Lellinger, comb. nov.

Gymnogramme ceratolepis var. *atirrensis* Donn. Sm. Bot. Gaz. **23:** 251. 1897. TYPE: Atirro, Pcia. Cartago, Costa Rica, 1800 ft alt, *Donnell Smith 6882* (US).

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Microgramma subg. Lopholepis (J. Smith) Lellinger, comb. & stat. nov.

Goniophlebium sect. *Lopholepis* J. Smith in Hooker & Bauer, Gen. Fil. *t. 51*. 1840. LECTOTYPE SPECIES: To fix the application of this name, I choose: *Polypodium piloselloides* L. (=*Microgramma piloselloides* (L.) Copel.), the only species of the original four illustrated at the time of publication.

Lopholepis (J. Smith) J. Smith, J. Bot. Hooker **4:** 56. 1842, *non* Dcne., 1839 (Gramineae), *nom. illeg.*

The species of *Microgramma* subg. *Lopholepis* are sparsely to densely scaly on both surfaces and their fertile laminae are markedly narrower than their sterile ones. The laminae of species of subg. *Microgramma*, on the other hand, are glabrous on both surfaces and the fertile laminae are only slightly narrower than the sterile ones. The subgenera seem to be very natural groups; it is useful to distinguish them at the subgeneric level, just as subgenera are maintained in *Polypodium*. Despite the differences between the subgenera, the species are more closely allied to one another than to the species of other genera. These relationships are obscured if one recognizes only the single genus *Polypodium sensu lato* and are just as hidden if all the subgenera are raised to generic level.

Microgramma subg. Solanopteris (Copel.) Lellinger, comb. & stat. nov.

Solanopteris Copel. Amer. Fern J. **41:** 75. 1951, as "*Solenopteris*." TYPE SPECIES: *Polypodium bifrons* Hooker (≡*Microgramma bifrons* (Hooker) Lellinger).

As Copeland noted when he described *Solanopteris*, its affinity is with *Microgramma*. Copeland claimed generic status for *Solanopteris* because it had sterile leaves with a fleshy, herbaceous texture (whatever that might be!) and with laxly and irregularly anastomosing veins with few included veinlets. These characters are, in my opinion, insufficient to distinguish *Solanopteris* from *Microgramma* generically, especially considering the species of *Solanopteris* discovered since Copeland wrote. The similarities in venation seem to me to be more important than the fact that the rhizome scales of *Solanopteris* are small and circular, like all those of some species of *Polypodium* subgenera *Goniophlebium* and *Marginaria*, both of which have venation no more complex than goniophlebioid. Both circular and elongate rhizome scales are known within subg. *Goniophlebium*, and so this does not appear to be a character of generic importance in the *Polypodiaceae sensu stricto*.

Microgramma bifrons (Hooker) Lellinger, comb. nov.

Polypodium bifrons Hooker, Fil. Exot. *t. 52*. 1859. TYPE: Near Archidoña, Pcia. Napo, Ecuador, *Jameson* (K not seen).

Microgramma brunei (Wercklé ex Christ) Lellinger, comb. nov.

Polypodium brunei Wercklé ex Christ, Bull. Soc. Bot. Genève II, **1:** 221. 1909. TYPE: Costa Rica, *Wercklé* (P not seen.)

This species and the preceding both belong to subg. *Solanopteris*.

Pteris daguensis (Hieron.) Lellinger, comb. nov.

Pteris orizabae var. *daguensis* Hieron. Bot. Jahrb. Engler **34:** 495. 1904. TYPE: Banks of the Río Dagua, Depto. El Valle, Colombia, 200–500 m alt, *Lehmann 8933* (B not seen; isotype US).

Thelypteris crassiuscula (C. Chr. & Maxon in Maxon) Lellinger, comb. nov.

Dryopteris crassiuscula C. Chr. & Maxon in Maxon, Amer. Fern J. **23:** 75. 1933. TYPE: Vicinity of La Palma on the road to La Hondura, Pcia. S. José, Costa Rica, 1500–1700 m alt, *Maxon 8040* (US).

Alan Smith (in herb.) has assigned this species to sect. *Uncinella* of subg. *Amauropelta*. Maxon and Christensen tentatively assigned it to subg. *Steiropteris*, but its pinnae lack keels between the lobes and somewhat hooked hairs occur on the costae and rachis.

Thelypteris gleichenioides (Christ) Lellinger, comb. nov.

Aspidium gleichenioides Christ, Bull. Herb. Boiss. II, **4:** 960. 1904. TYPE: Volcán Barba facing the Pacific, Pcia. Heredia, Costa Rica, 2700 m alt, *Pittier 1935* (P not seen; isotype US).

The original description cites Tonduz as the collector, but the Pittier number is surely the same material, being collected at the same place and on the same date. Christ (Bull. Herb. Boiss. II, **6:** 161. 1906) considered this specimen to be *Aspidium nervosum* Klotzsch, contradicting his earlier, and in my opinion correct, determination. This species differs from *T. nervosa* (Klotzsch) Tryon in having non-falcate segments and by growing at much higher altitudes.

Thelypteris inaequans (C. Chr.) Lellinger, comb. nov.

Dryopteris euchlora var. *inaequans* C. Chr. K. Danske Vidensk. Selsk. Skr., Natur. Math. Afd. VII, **10:** 150. 1913. LECTOTYPE: To fix the application of this name, I choose: Upper Caldera watershed, Holcomb's trail above Boquete, Pcia. Chiriquí, Panama, 1650–1925 m alt, *Maxon 5674* (US). The other syntype is: Isla Ometepe, Lago Nicaragua, Depto. Rivas, Nicaragua, *Wright* (US).

Thelypteris prolatipedis Lellinger, nom. nov.

Dryopteris coarctata var. *longipes* C. Chr. K. Danske Vidensk. Selsk. Skr., Natur. Math. Afd. VII, **4:** 292. 1907, *non T. longipes* (Blume) Reed. TYPE: Alto de Alegrías near Frontino, Depto. Antioquia, Colombia, 2800 m alt, 22 Oct 1884, *Lehmann XXI* (B not seen; isotype US).

TYPE: A renaming of *Dryopteris coarctata* var. *longipes* C. Chr., and so based on the type of that name.

This species differs from *Thelypteris coarctata* (Kunze) Tryon in its glossy, reddish brown, clathrate rhizome scales, which have a few whitish setae mostly on the margin. Besides the isotype of *D. coarctata* var. *longipes*, I have seen only two collections from Volcán Barba, Pcia. Heredia, Costa Rica (*Valerio 212*, US; and *Lellinger 1714*, CR, UC, US). None of the specimens has indusia or appears to have had indusia. According to A. R. Smith (Amer. Fern J. **64:** 90. 1974), species of sect. *Amauropelta* have indusia, and so *T. prolatipedis* appears to be an exception, but by all other characters it does belong in sect. *Amauropelta*.

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SHORTER NOTES

HOW FAST DOES A STAGHORN FERN GROW?—For approximately five years I have had a Staghorn Fern (*Platycerium bifurcatum*) growing in my air-conditioned office. The plant is about six or seven years old and is mounted with sphagnum moss on a cypress plaque. The office temperature is set for 76° F and the relative humidity is about 50%. The plant receives light from four banks of fluorescent lights (Westinghouse Cool Light), and the illuminance at noon is 85 ft-c.

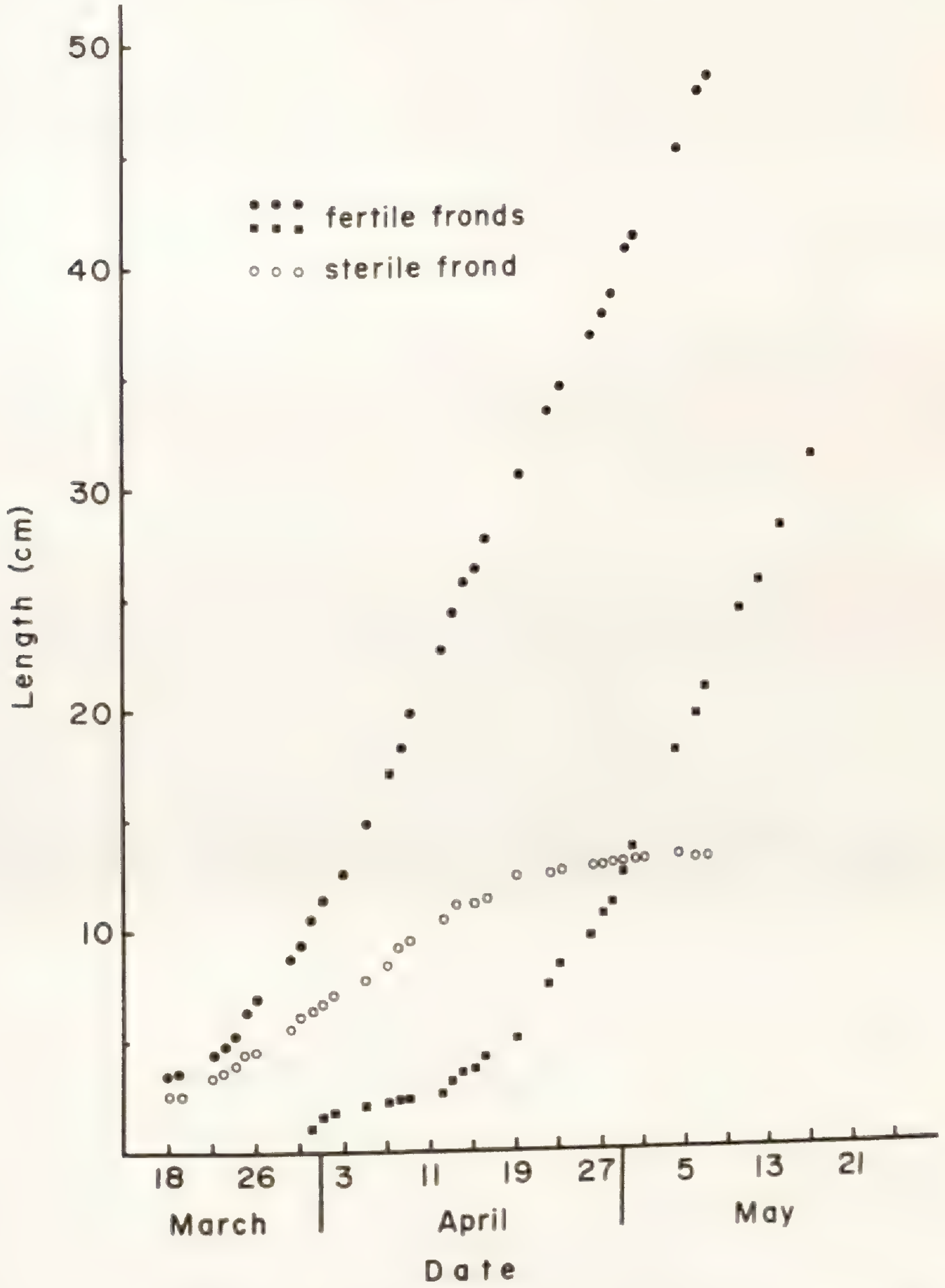

FIG. 1. Growth in length of two fertile and one sterile frond of *Platycerium bifurcatum*.

The plant is hung on the wall during the week. On Friday afternoon it is placed in a sink and watered thoroughly, where it remains until Monday morning, when it is again watered thoroughly, allowed to drain, and is returned to the wall. It is fertilized about three times a year with about 100 g of Milorganite. Pests have not been any difficulty.

How well does a Staghorn Fern do under these apparently rather unfavorable conditions? When measurements were begun on 18 March 1976, the fern had one sterile and eight fertile fronds. The longest fertile frond was 78.0 cm. I followed the growth of two fertile and one sterile frond for about two months. The results are shown in *Fig. 1*. At the steepest part of the curves, the fertile fronds were growing about 10 mm per day and the sterile frond was growing about 3 mm per day.

Assuming that the sterile frond is semicircular, the amount of surface added during the period of rapid growth (26 March to 19 April) was calculated to be 254.7 cm^2 for this 25-day period. It was assumed that the shape of the fertile fronds could be represented by a rectangle flanked on two sides by triangles. For the same time period, the amount of surface area added was calculated to be 270.0 cm^2. Thus, in terms of tissue added each day, there is very good agreement between the two frond types.—*D. I. Hamasaki, 9841 S.W. 60 Court, Miami, FL 33136.*

TWO ADDITIONS TO THE FERN FLORA OF CHIHUAHUA, MEXICO.—The most thoroughly documented fern flora in northern Mexico is that of the state of Chihuahua. Few additions to this flora have been reported since the 1962 publication of Knobloch and Correll's "Ferns and Fern Allies of Chihuahua, Mexico." On June 10–11, 1976, Mr. Lyle McGill and I collected extensively in the canyon below the 300 m high Basaseachic Falls in southwestern Chihuahua. This magnificent canyon has been visited infrequently by botanists, judging by the few collections cited from this area by Knobloch and Correll. Two species new to the flora of Chihuahua were found. The first, *Asplenium sessilifolium* Desv., occurs on shaded, west-facing, rocky slopes in mixed conifer-hardwood forest, ca. 2 km south of the falls at ca. 1800 m elevation (*McGill & Reeves R4937*, ASU). This species was previously known from northern South America through Central America as far north as the Mexican States of Durango, Hidalgo, and Sinaloa. The second species, *Pteris cretica* L. was found on shaded, west-facing slopes in deciduous hardwood forest, ca. 1-2 km south of the falls among boulders at ca. 1800 m elevation. A lovely, variegated form occurs ca. 2 km below the falls (*McGill & Reeves R4947*, ASU). This species is widespread in the world tropics, having been known previously as far north in Mexico as Nuevo Leon and Hidalgo. This is the first report for the species in northwestern Mexico. Travel in Mexico was supported by NSF Grant BMS-7501417 to Dr. Thomas H. Nash III, Arizona State University.—*Timothy Reeves, Department of Botany and Microbiology, Arizona State University, Tempe, AZ 85281.*

AN OCCURRENCE OF PTERIS MULTIFIDA IN VIRGINIA.—As early as 1961, on my way to work in Charlottesville, Virginia, I occasionally walked past a four foot high brick retaining wall bordering a sidewalk. This east-facing wall in a shaded residential district was in a state of slight disrepair, and was probably as old as the surrounding houses, which were built in the early and mid-nineteenth century. Among the weedy plant species (*Lamium amplexicaule* L., *Duchesnia indica* (Andrz.) Focke, and a yellow *Oxalis*) which grew scattered in the mortar and crevices of the wall, were about nine clumps of a peculiar, slender fern with striking symmetry. Quite by accident, I ran across a picture of it in H. L. Blomquist's "The Flora of North Carolina" (1934). It was *Pteris multifida* Poir., the Spider Brake, a native of eastern Asia, but an introduction in the southeastern United States, where it occurs from Texas and Florida northward to Craven and Wayne counties in eastern North Carolina. At its northern limits it is usually found on old walls and masonry.

Specimens were collected in 1964 and 1967 from plants rooted in mortar between bricks in the lower, damper part of the wall, which retained a steeply sloping lawn. The ferns appeared to be evergreen, in spite of winters with low temperatures of 5° to 10° F, although some of the pinnae died at their tips.

A conversation with a former resident of the house at 425 North First Street where the ferns grew revealed no knowledge of any neighborhood fern cultivation, but only that the wall used to be cleaned up years ago by "pulling that stuff out of there." However, the rootstocks were deeply imbedded, and the plants were still present in 1968. The few local greenhouses are small, commercial, and located a mile or more distant from the location in different direction, so that the derivation of this colony is puzzling. Page's Greenhouse, which went out of business in 1975, was situated two miles to the west and had a number of clumps of *P. multifida* growing from an inside rock wall by a pool, where the plants appeared spontaneously. It was not a greenhouse weed there to the extent that another fern, *Cyclosorus dentatus* (Forsk.) Ching, a widespread native of the tropics, was.

Dr. Edgar T. Wherry in a letter (1968) from Philadelphia said: "It has been coming up for years in crevices in the wall of the 'Fern House' at the Morris Arboretum here, but that represents a carrying of spores only a few feet, and moreover it is never far from the warm foundation-wall, so I never felt it was worth notice."

The Virginia colony died inexplicably in 1969 or 1970, and the wall was removed during new construction in the early 1970's. Whether this occurrence is too tenuous to register the extension of the species northward into "Gray's Manual range" is a question. However, it is antedated by a specimen I have seen that was collected on May 1, 1956 in crevices in brick of sewer, Second Street above A Street, NE, Washington, D.C., *F. J. Hermann 12605* (US). On April 15, 1976, I made a brief visit to this location, but did not see the plant or site as described.

Vouchers of the Charlottesville plants were deposited in the herbarium of Longwood College (FARM) and were sent to Dr. Wherry.—*Charles E. Stevens, 615 Preston Place, Charlottesville, VA 22903.*

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Manuscripts should follow recent Journal style and should be prepared in accordance with the AIBS (1964) "Style Manual for Biological Journal" or the AIBS (1972) "CBE Style Manual." For major articles with more than one literature reference, use the "name and year" system for bibliographic references and the American Standards Association list of bibliographic abbreviations (AIBS, 1964, pp. 82-87), which may be supplemented by the list of Schwarten and Rickett (1958), or by those in the comprehensive "Botanico-Periodicum-Huntianum" (Lawrence et al., 1968). Put a single reference in a footnote or in the text. For shorter notes and reviews, put all references in parentheses in the text. Abbreviations of the names of herbaria should follow the list of Holmgren and Keuken (1974).

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Asplenium × herb-wagneri — A Collective Epithet for A. pinnatifidum x trichomanes

W. CARL TAYLOR* and ROBERT H. MOHLENBROCK**

On the basis of a specimen collected from Pine Hills, Union County, Illinois on 12 October 1967, Wagner and Wagner (1969) described a new *Asplenium* hybrid arising from a cross between the amphidiploid *A. pinnatifidum* and a diploid race of *A. trichomanes*. Voucher material of this hybrid is morphologically intermediate between the putative parents. *Asplenium pinnatifidum* × *trichomanes* is known to exist only as a sterile triploid, but chromosome doubling could presumably form an allohexaploid capable of viable spore production.

FIG. 1. Juvenile fronds from the type of *Asplenium* × *herb-wagneri*, *Wagner 67024*, MICH. FIG. 2. Mature fronds cultivated from the type of *A.* × *herb-wagneri*.

A second plant of *A. pinnatifidum* × *trichomanes* was discovered at McBride's Bluff, Martin County, Indiana on 22 August 1970 (Gastony, 1971). Careful field work will likely reveal additional locations for this plant.

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Since this hybrid has not received a latin description and collective epithet, it seems appropriate and useful to provide the following.

Asplenium × herb-wagneri Taylor & Mohlenbrock, hybr. nov. **Figs. 1–2.**

Hybrida ex *Asplenio pinnatifido* Nutt. et *A. trichomane* L. Rhizoma breve repens vel erectum; paleae clathratae. Frondes delicatae patentes lineares pinnatae inferne pinnatifidae vel crenato-serratae apicem versus, usque ad 17 cm longae, usque ad 1.8 cm latae membranaceae caudato-attenuatae ad apicem; stipes tenuis nitens atroporphyreus; rachis leviter maeandriformis plerumque atroporphyrea infra medium viridis apicem versus; pinnae separate vel remotae, paribus usque ad 15 subopppositis vel alternatis, suborbiculatae vel ovatae vel flabellatae, usque ad 9 mm longae, usque ad 0.9 mm latae, obtusae ad apicem denticulato-serrulatae vel crenulatae cuneatae ad basim, venis libris. Sori usque ad 2.5 mm longi; sporae abortivae.

TYPE: In crevice of chert outcrop near McGee Hill Overlook, Pine Hills, Union Co., Illinois, Sec. 21, R3W, T11S, 12 Oct 1967, *W. H. Wagner, Jr. 67024* (MICH).

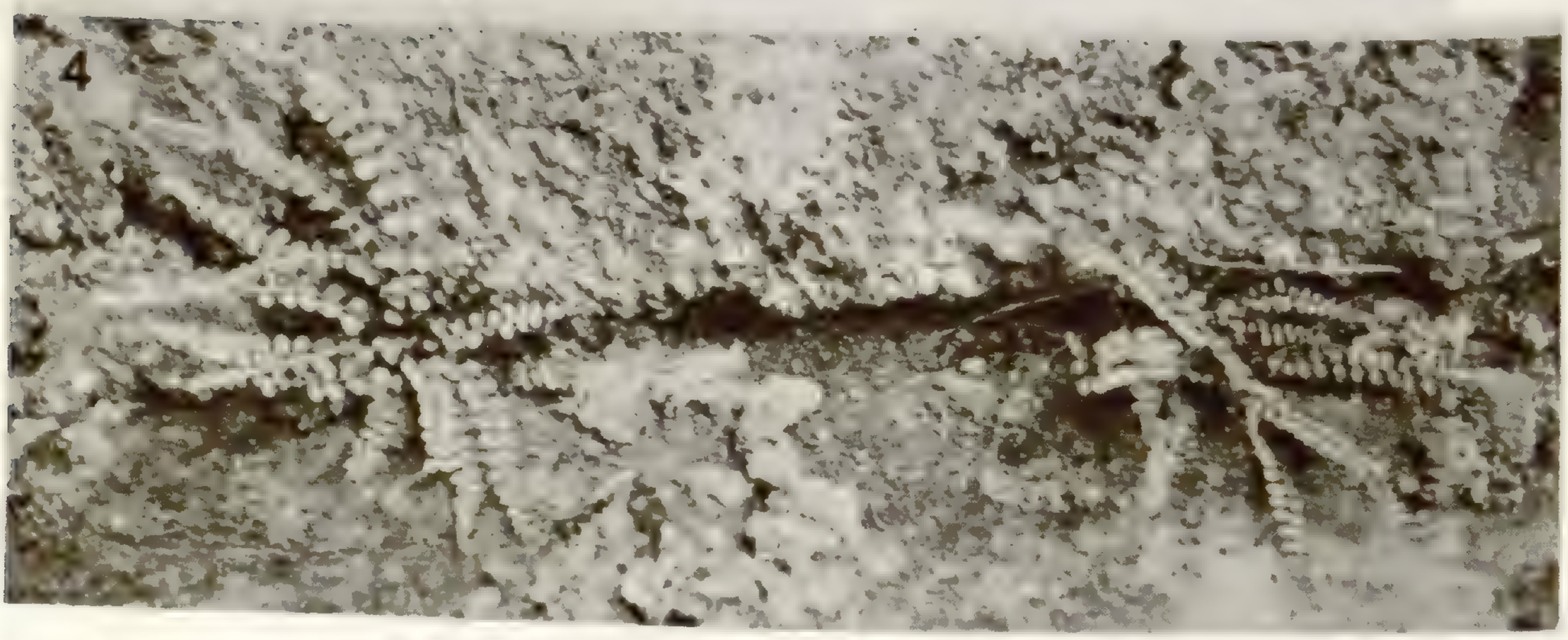

FIG. 3. Portion of plant of *A. × herb-wagneri* from Martin County, Indiana, *Gastony 949*, IND. FIG. 4, *Asplenium × herb-wagneri* (left) and *A. trichomanes* (right) growing at McBride's Bluff, Martin County, Indiana. (photo by G. J. Gastony)

PARATYPE: Pocket on a south-facing sandstone cliff, McBride's Bluff, along east fork of White River, ca. 6 miles north of Shoals, Martin Co., Indiana, 22 Aug 1970, *G. J. Gastony 949* (IND, US).

We are grateful for the opportunity to name this hybrid in honor of Dr. Warren H. Wagner, Jr., who first recognized and described it.

The discovery of this hybrid is significant because of its bearing on the interpretation of *A. stotleri,* which was previously thought to have originated from a cross between *A. pinnatifidum* and *A. trichomanes* (Wherry, 1961 p. 162). *Asplenium stotleri* is now believed to be only a round-lobed form of *A. bradleyi* (Wagner & Wagner, 1969).

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An Apical Cell in the Shoot Apex of Isoëtes tuckermanii

ERIC E. KARRFALT*

Well defined apical cells in the meristems of pteridophytes other than *Isoëtes* typically have a simple geometric shape, a relatively large size and nucleus, and a high degree of vacuolation. In radially symmetrical apices, the apical cell is located at the center of the apex. But the most important requirement of an apical cell is that it be the source from which all cell lineages in the apex are derived. The recent history of segmentation of an apical cell may be deduced from the geometrical relationships and relative thickness among the walls of the surrounding cells (Bierhorst, 1977). The most recently formed cell walls are the thinnest; older walls are thicker due to the deposition of additional primary wall material as cells become subdivided into groups or packets of cells.

The shoot apex of *Isoëtes* was originally described by Hofmeister (1862) as having a single apical cell which was the ultimate origin of all other cells in the shoot. Using various species including the one which Hofmeister studied (*I. lacustris*), later workers have either denied the existence of a single apical cell (Bruchmann, 1874, Hegelmaier, 1874; West & Takeda, 1915; Bhambie, 1957) or have allowed that at least in some cases such a cell may be present (Scott & Hill, 1900; Lang, 1915; Paolillo, 1963). Scott and Hill suggested that Hofmeister may have been influenced in his interpretation by the fact that the apical cell was the only type of apical organization known at that time, but they were careful to point out that occasionally an apical cell may be present. Scott and Hill found several examples of what they thought might be apical cells, but they could not determine if the large size and central position of these cells were stable or if these properties would have been lost in the course of further activity of the meristem.

The present report confirms the existence of an apical cell at least in some specimens of *I. tuckermanii* A. Br.

METHODS AND MATERIALS

Bierhorst (1977) has clearly demonstrated the superiority of using cleared, thick, free hand sections to study fern apices. Such preparations give a full view of the surface of the apex where the geometry and thicknesses of the cell walls are most reliably seen, and would undoubtedly have been advantageous in the present study. Unfortunately, the present material was prepared before Bierhorst's paper appeared, and only serial paraffin sections were used. The material examined here was part of a collection of about 600 individuals of *I. tuckermanii* (*Karrfalt 8*, BHO) from eastern Massachusetts.

OBSERVATIONS

In the course of other studies with *Isoëtes* (e.g., Karrfalt & Eggert, 1977), four relatively old plants were found which showed an apical cell in cross sections of the shoot apex. A specific search for apices with apical cells, however, has revealed that the occurrence of such apices is infrequent and apparently not corre-

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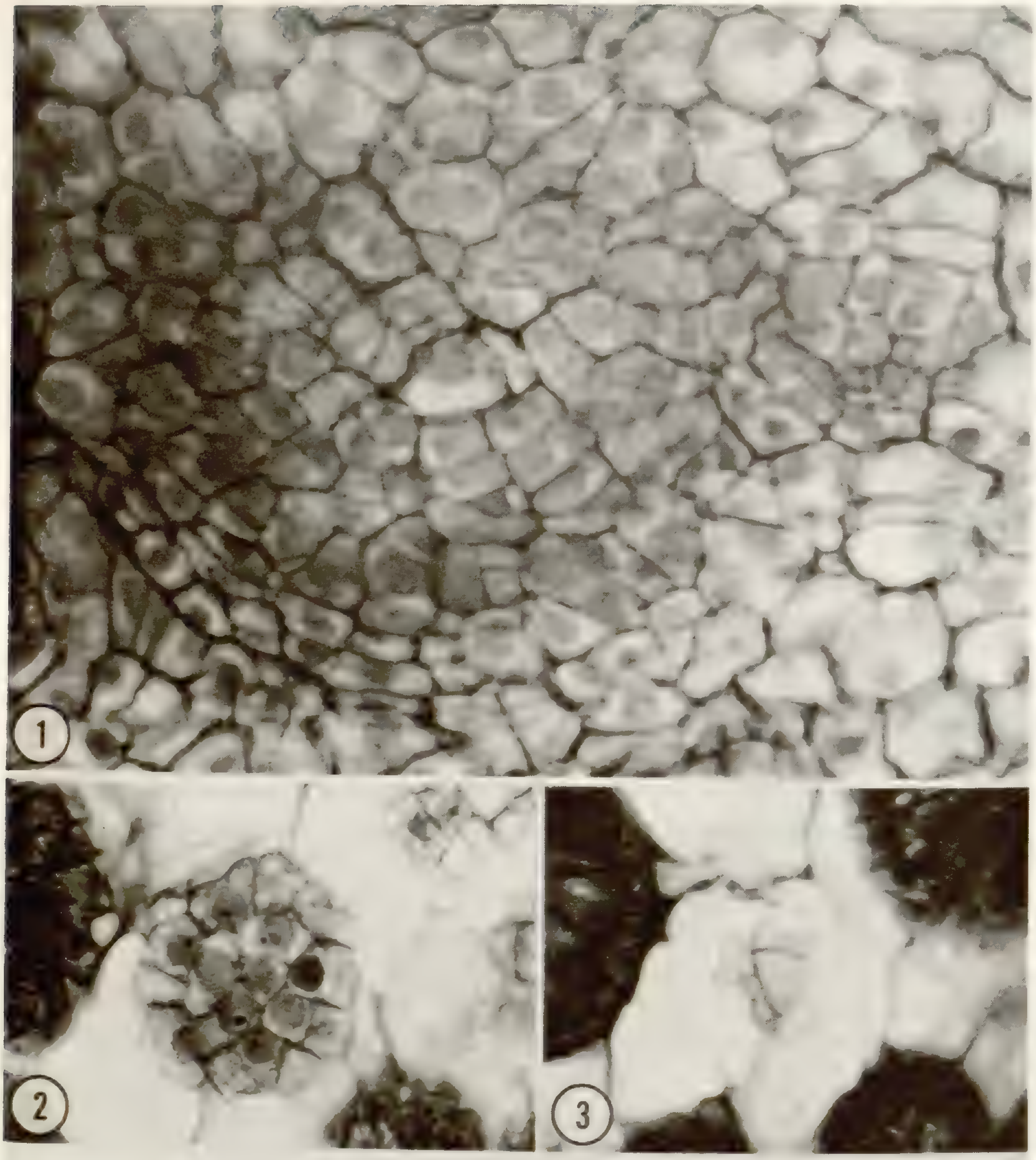
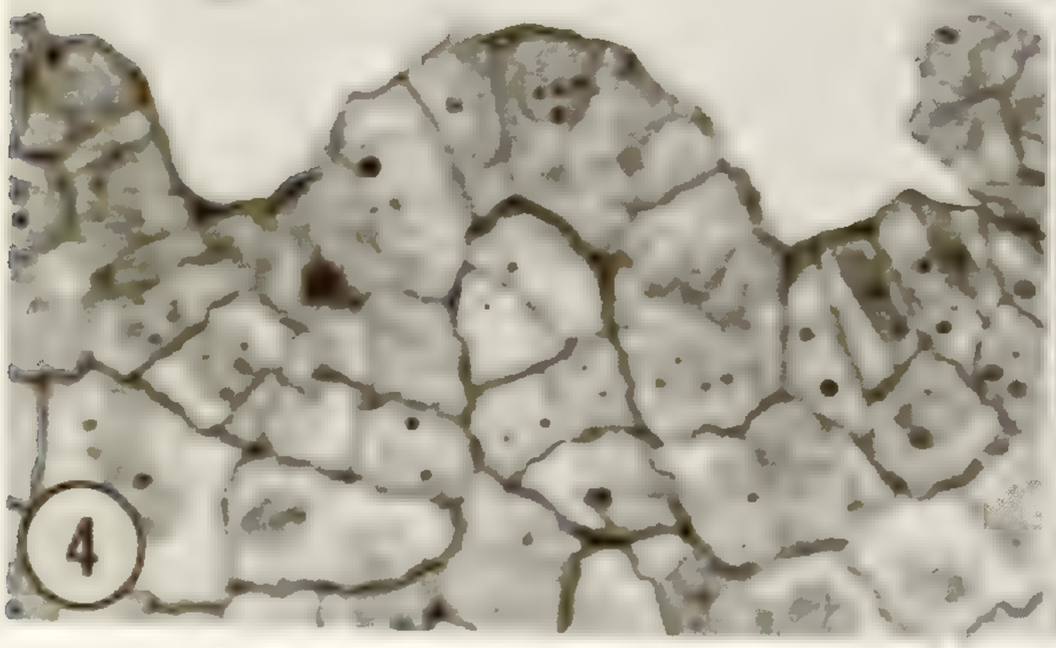
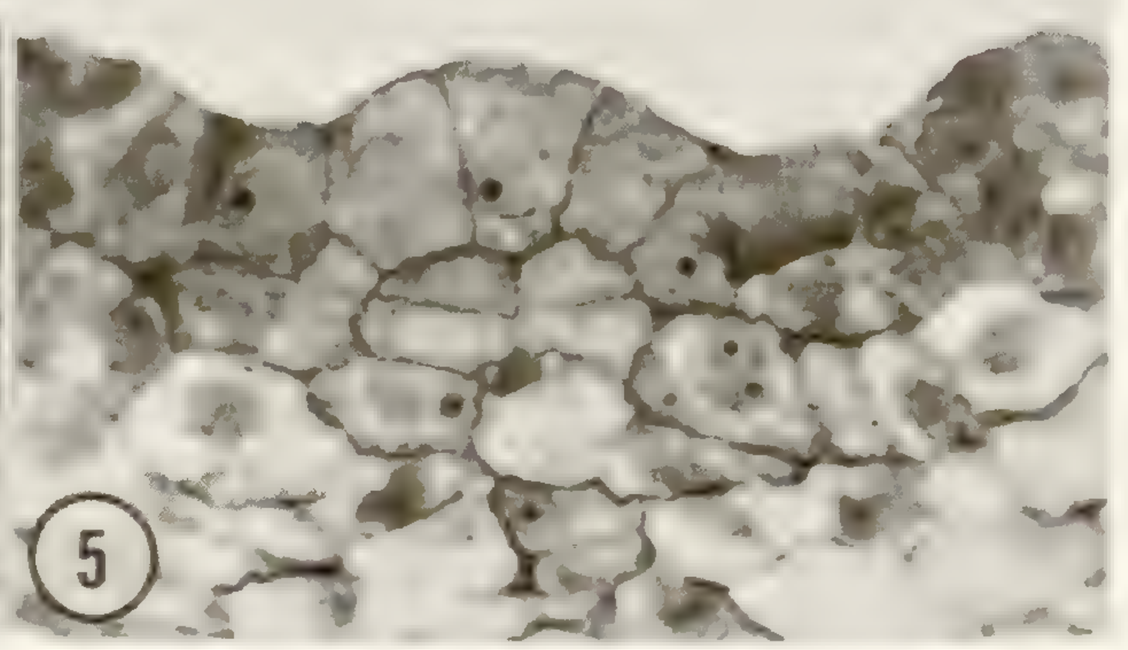
lated with any particular structural or developmental circumstance, except that none were found in plants younger than about five years old (ages estimated according to Karrfalt & Eggert, 1977). Of ten relatively old plants which were sectioned longitudinally in a search for apical cells, five showed a large cell, which may have been an apical cell, at the summit of the median section; but of seven other plants which were sectioned transversely, only one showed a cell which could be confirmed as an apical cell on the basis of its apparent history of segmentation. Presumably, therefore, at least not all and possibly none of the cells which had the appearance of being apical cells in the longitudinal sections actually were such.

The shoot apex shown in cross section in *Fig. 1* has the best developed apical cell which I have found. In this specimen, the apical cell is conspicuously larger, has a somewhat larger nucleus, and is more highly vacuolated than the surrounding cells. It is located quite precisely in the center of the relatively flat apical dome. The derivatives of the apical cell are arranged about it in more or less distinct radial files. The existence of these radial files indicates that cell divisions have had a regular orientation in this apex for some time. As seen at lower focal levels within the apical cell, it tapers proximally to a point (i.e., the shape of the cell is essentially that of an inverted pyramid). The apical cell appears to have at least three and possibly four cutting faces. Just to the right of the apical cell is a smaller cell which has apparently been recently cut off from the apical cell. This small cell is approximately opposite two radial files to its right; probably it would have divided parallel to these radial files and thus contributed an additional cell to each. This sequence of divisions appears to have given rise to the two cells immediately below the apical cell in *Fig. 1* because the combined width of these cells matches that of the apical cell plus that of the small cell most recently derived from it. Possibly the two cells above the apical cell were also produced in this way. The relationship between the apical cell and those to its left in the figure is obscure, but conceivably the cells on the left were originally derived from the apical cell in the same manner as that suggested for the other cells surrounding the apical cell.

Figures 2 and *3* are adjacent cross sections of the same apex. The cell in the center in these figures has the shape of a nearly regular, inverted, triangular pyramid. It differs from the surrounding cells only in its shape and central location, but the arrangement of the surrounding cells suggests that its location has been constant at least during the most recent development of the apex. The cell just above the central, triangular cell in *Fig. 2* apparently shared a common origin with the triangular cell, and the form of the two cells to the left of the triangular cells suggests that they may have resulted from the division of a cell similar to that above the triangular cell. If the next division of the triangular cell were to have been comparable to the previous two, then a cell would have been cut off to the lower right. The wall on the lower right is slightly shorter than the other two; and at least in ferns with three-sided apical cells, the apical cell always divides by a new wall formed parallel to the shortest of the three walls prior to the division (Bower, 1889; Lintilhac & Green, 1976).







FIGS. 1-5. Shoot apical meristems of *Isoëtes tuckermanii*. FIG. 1. Cross section, × 650. FIGS. 2-3. Serial cross sections, × 500. FIGS. 4-5. Median longitudinal sections, × 500.

The cells at the tops of the apical domes in *Figs. 4* and *5* may represent apical cells, but in longitudinal sections it is not possible to definitely identify an apical cell unless there are conspicuous differences in size or contents between the cell at the summit of the apex and those below it. No such cell was encountered in this study. Theoretically the appearance of these apices in cross section could be reconstructed from an accurate series of camera lucida drawings of the longitudinal sections, and the history of segmentation of the suspected apical cell then deduced from the reconstructed cross section, but the time consumed by such an analysis would be excessive. Most of the apices which were sectioned longitudinally seem to show a few stable, subsurface initials within the apical dome; in *Fig. 4* there is only one, and in *Fig. 5* there are two. The common walls between the surface and subsurface initials in *Fig. 4* are unusually thick. These thick walls presumably are made up of numerous layers of primary wall material laid down subsequent to regularly oriented cell divisions. The superficial cells have apparently been dividing strictly anticlinically, and the subsurface initial has apparently been cutting off cells proximally.

DISCUSSION

The illustrations given by Scott and Hill (1900) of large, centrally located cells which may represent apical cells do not show any regular arrangement of the surrounding cells which could be interpreted as evidence of a regular history of segmentation. Thus these large cells probably do not represent apical cells. The critical evidence presented here is the regular arrangement of the cells surrounding the apical cells (*Figs. 1-2*).

Obviously the rarity of the occurrence of an apical cell in *Isoëtes* negates Hofmeister's characterization of the shoot apex of *Isoëtes* as being of the apical cell type. A true apical cell exists only in exceptional cases, but the fact that even these exceptional cases have not been definitely confirmed until now has left the implication that Hofmeister was not simply generalizing on the basis of two few specimens, but that his observations were in error and his illustrations were not accurate. Undoubtedly Hofmeister was capable of error, but his observations of the "apical cell" of *Isoëtes* are not necessarily faulty. There is in fact every possibility that he saw exactly what he described and illustrated concerning the shoot apex of *Isoëtes*. One of his drawings in particular (Fig. 8, plate 48) compares almost exactly with *Figs. 2* and *3*.

Two rather minor additional comments might be made about Hofmeister's description. He states that the derivatives of the apical cell ". . . form a spiral, winding round the middle point of the primary cell, which spiral, as far as observations have hitherto gone, is always a right-handed one," and this is exactly the sequence of segmentation shown in *Fig. 2*. On the other hand Hofmeister also asserted that the number of cutting faces on the apical cell equalled the number of lobes on the corm and that division walls of the apical cell were always at right angles to the nearest furrow on the surface of the corm. Possibly these relationships existed in his material, but both of the plants shown here in *Figs. 1-3* were two-lobed.

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REVIEW

"Classification of Athyrium and allied genera of Japan," by Masahiro Kato, Bot. Mag. Tokyo **90:** 23-40. 1977.—Generic concepts in the genus *Athyrium* and its relatives that have been published in the past thirty years have varied markedly. Some treatments have maintained only a single, large genus *Athyrium,* whereas others have recognized several segregate genera based mostly on gross morphology. Few of these studies have been inclusive attempts to study and understand the complex as a whole. The present paper remedies this; it utilizes more characters of morphology and anatomy from more species than have past studies. Kato's conclusions are presented in a workable key, generic synonymies, and copious notes. Four genera are recognized. *Athyrium* includes *Anisocampium, Kuniwatsukia, Pseudathyrium,* and *Pseudocystopteris. Deparia* includes *Athyriopsis, Dryoathyrium,* and *Lunathyrium* as sections, as well as sect. *Deparia. Diplazium* includes *Allantodia, Dictyodroma, Diplaziopsis, Hemidictyum, Monomelangium,* and *Rhachidosorus. Cornopteris* is the fourth genus. *Cystopteris* is also included in the key, and its relationship to *Athyrium* is discussed. *Athyrium* and *Diplazium* are broken up into informal groups, based on the author's knowledge of the Old World species. New World species, especially of the latter genus, would require a different, more extensive classification, but fall beyond the scope of the present paper.—*D.B.L.*

Ciné Analysis of the Medullary Bundle System in Cyathea fulva[1]

DAVID C. ADAMS*

In recent years there has been a renewal of interest in the anatomy of tree ferns of the families Cyatheaceae and Dicksoniaceae. While the paleotropical representatives of these families have received considerable anatomical study in the past (Ogura, 1927, 1972; Godwin, 1932; Mehra & Singh, 1955), it is only recently that similar attention has been directed towards tree ferns of the New World tropics (Lucansky, 1974; Lucansky & White, 1974).

The vascular anatomy of the tree fern rhizome is characteristically a dictyostele with the individual meristeles surrounded by a thick layer of sclerenchyma. In addition, the squamate genera of the Cyatheaceae (those bearing scales rather than trichomes as stem and petiolar indument) all possess numerous additional vascular bundles in the medullary and, in some genera, cortical regions. Each of these auxiliary strands is, in turn, partially surrounded by a sclerenchyma sheath (Lucansky, 1974).

While much work has been and is being done on the main meristele and on comparative aspects of the stem in general, little attention has been given to the three-dimensional architecture of the auxiliary system and its functional significance. This is primarily due to the limitations imposed by the methods previously employed. Sectioning techniques sufficient for the study of the main meristele are, as a rule, not adequate for studying the anastomosing medullary network over long distances.

This study examines in three dimensions the medullary auxiliary network of *Cyathea fulva* (Mart. & Gal.) Fée, using the technique of surface ciné photography (Tomlinson, 1970; Zimmermann & Tomlinson, 1974). In addition, the possible functions of these bundles are discussed.

MATERIALS AND METHODS

Cyathea fulva ranges from southern Mexico to Panama, Colombia, and Venezuela, and grows at 800–4200 (primarily 1500–2500) m elevation. It is found associated with forests of *Liquidambar, Podocarpus*, and *Quercus* (Tryon, 1976). The specimen used in this report was collected in a *Liquidambar* forest at 1250 m elevation near Misantla in the State of Vera Cruz, Mexico. The trunk was ca. 3 m long, of which about two-thirds (including the basal, apical, and mid-trunk portions) was brought back for study. Voucher specimens are on file at the Gray Herbarium, Harvard University, Cambridge, Massachusetts.

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[1]Based on research conducted for the writing of a senior thesis submitted to the Department of Biology, Harvard University in partial fulfillment of the honors requirements for the A.B. degree. Grateful appreciation is expressed to Dr. P. B. Tomlinson for assistance in the production and analysis of the ciné films, to Dr. Rolla Tryon for assistance in the collection and identification of the specimen, and to Monika Mattmuller (Harvard Forest) and Martin Kalish for the photographs.

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The surface ciné photography method consisted of placing a long, rectangular block of stem tissue in a modified sliding microtome with a 16 mm Paillard-Bolex ciné camera mounted above and focused on the transverse surface. Single frames were taken of the cut surface after thin sections (average 350- 400 μm) were successively sliced from the specimen. The advantages of this technique are: (1) it allows the recording of several thousand cross-sectional views without requiring

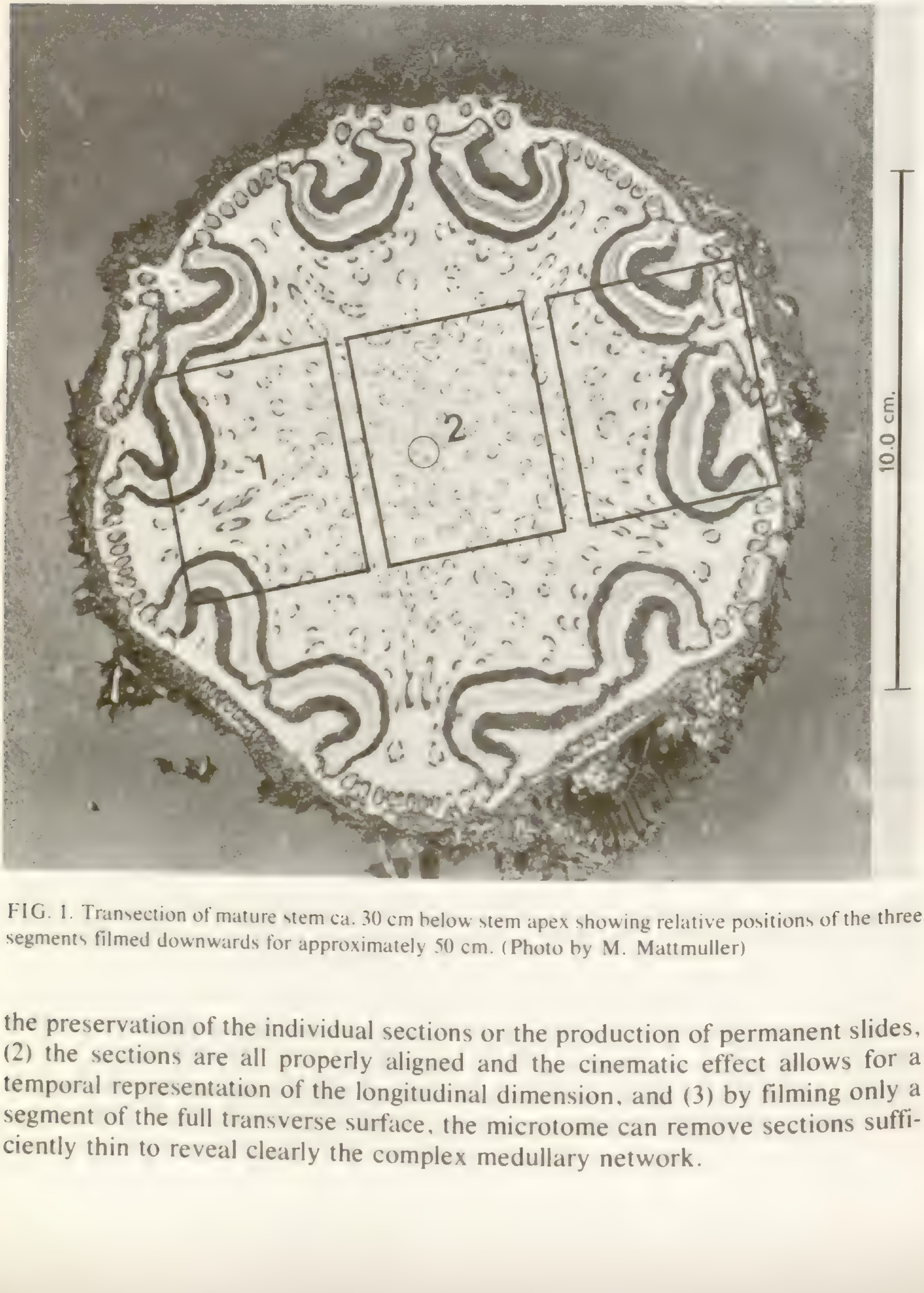
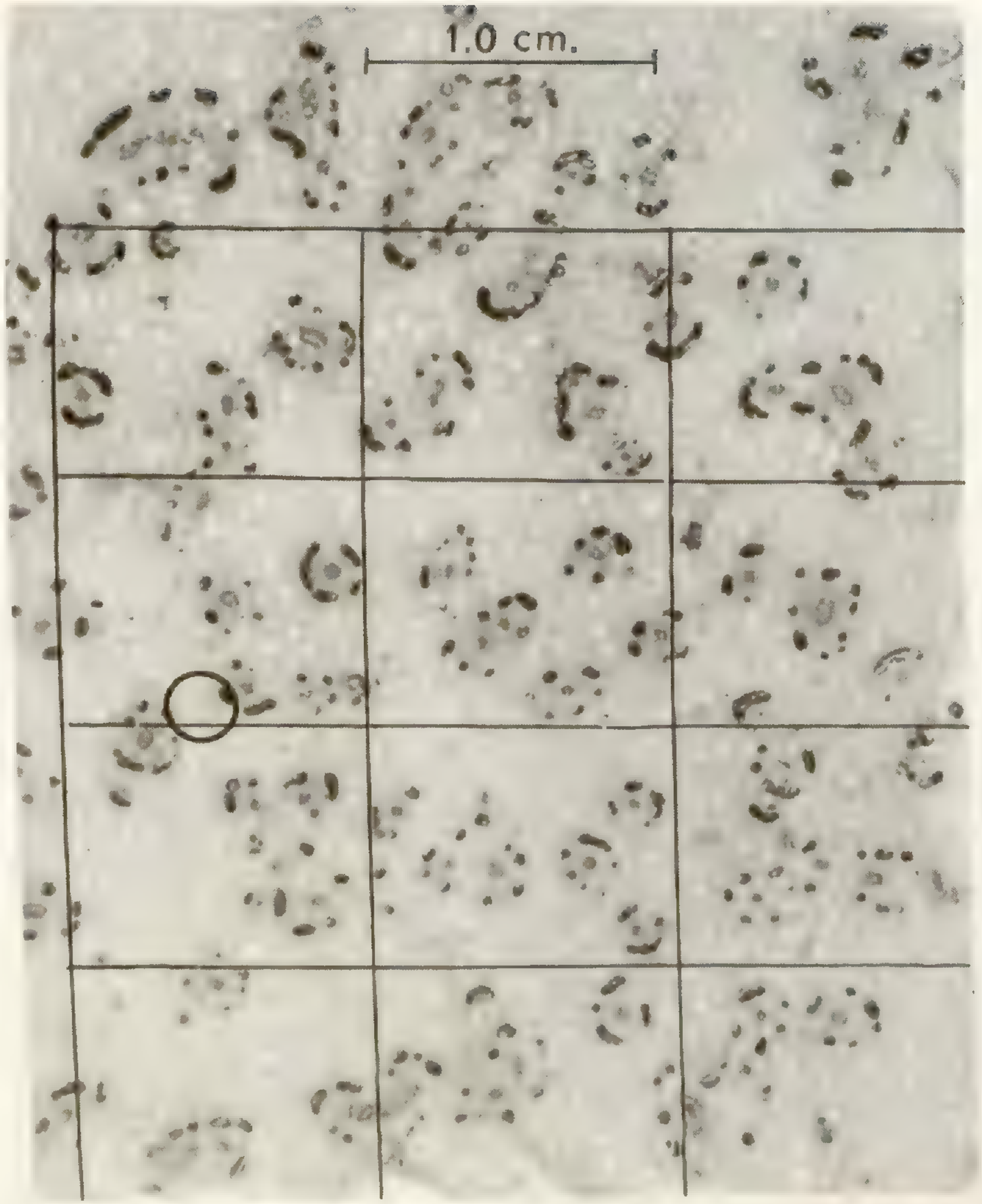


FIG. 1. Transection of mature stem ca. 30 cm below stem apex showing relative positions of the three segments filmed downwards for approximately 50 cm. (Photo by M. Mattmuller)

the preservation of the individual sections or the production of permanent slides, (2) the sections are all properly aligned and the cinematic effect allows for a temporal representation of the longitudinal dimension, and (3) by filming only a segment of the full transverse surface, the microtome can remove sections sufficiently thin to reveal clearly the complex medullary network.



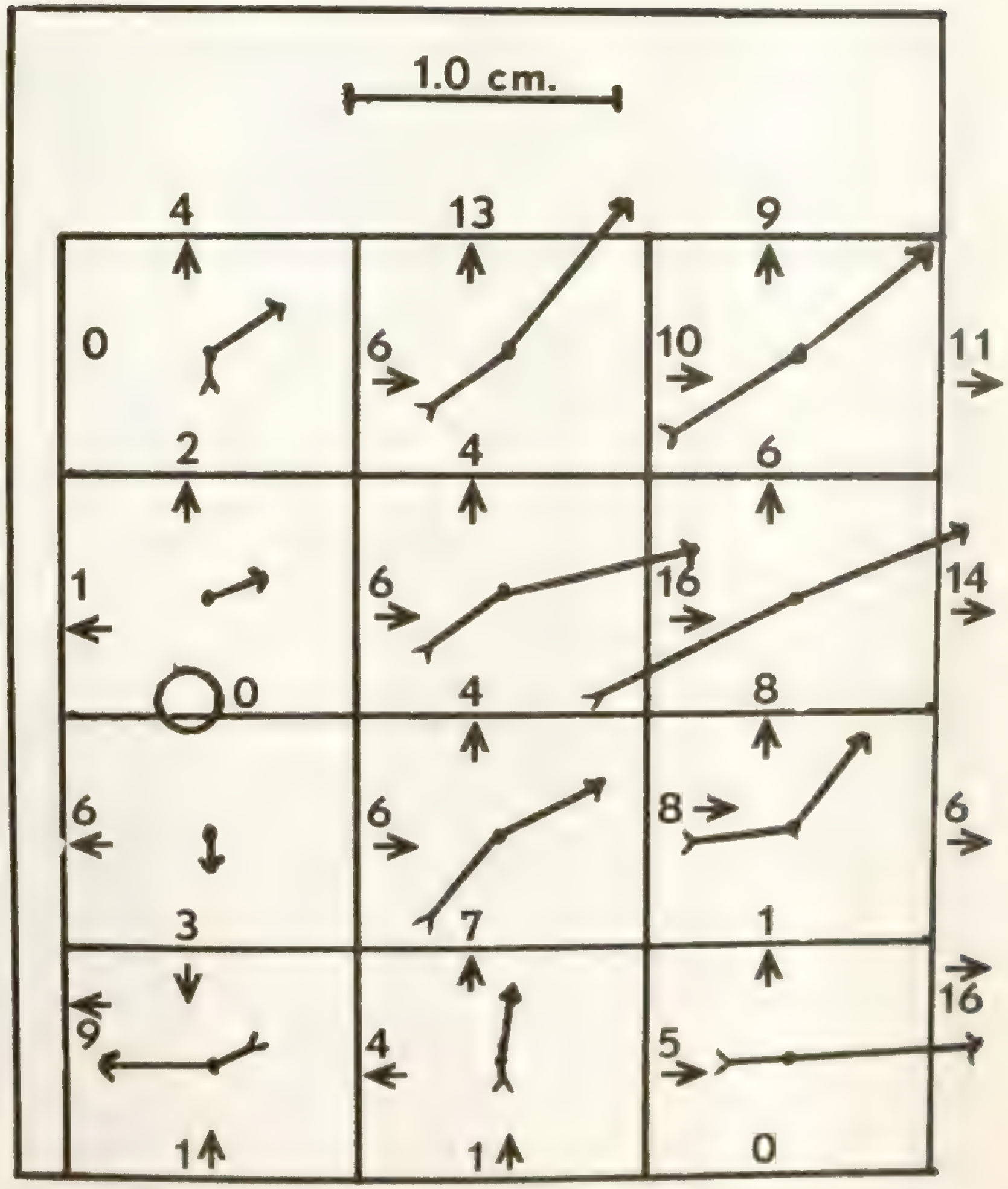


FIG. 2. Transection of central zone (Segment 2) showing the 12 quadrates studied, with the net numbers and directions of bundle crossings and the vectoral representation of bundle "drift" at the right. (Photo by M. Kalish)

The films of the three segments were analysed using two different methods. In the peripheral regions of the pith (*Fig. 1*, segments 1 and 3), the positions of the individual bundles were plotted on the basis of radial displacement (distance from the outside edge of the segment) versus longitudinal displacement (as indicated by the frame number calibrated via a factor representing average section thickness), thus allowing a precise quantitative tracing of the course of individual bundles over a considerable length of stem (*Fig. 4*). The courses of the bundles in the central region of the pith (*Fig. 1*, segment 2) were studied by dividing the surface

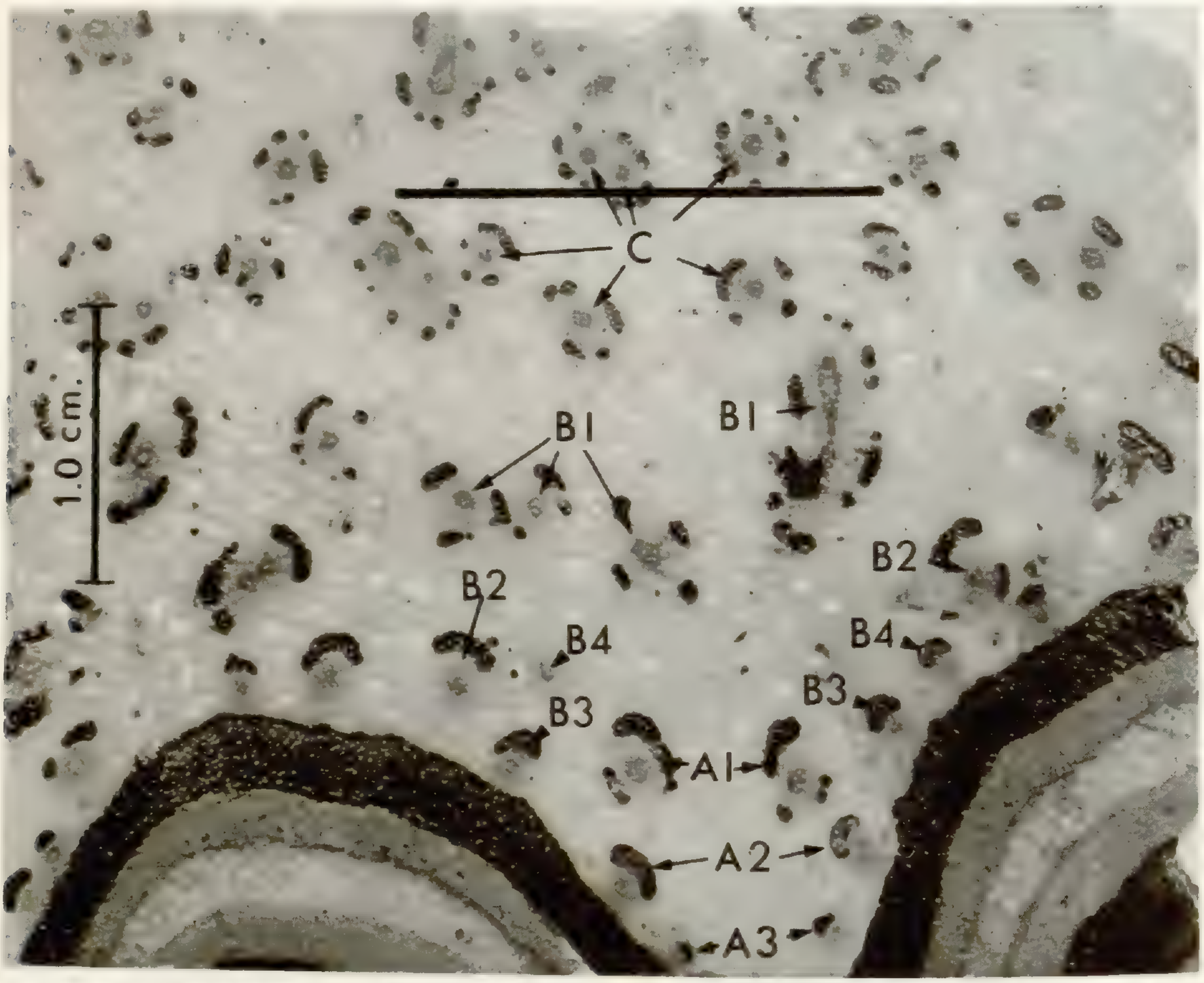


FIG. 3. Transection of Segment 1 showing the various A, B, and C bundles numbered in order of their subsequent departure through the leaf gaps. The edge of the central system is indicated by a line. (Photo by M. Kalish)

into twelve smaller quadrates and noting the net number and direction of bundles crossing these quadrate boundaries. These values were then combined to give a vectoral representation of the degree of bundle "drift" in the various parts of the central region. (*Fig. 2*).

RESULTS AND DISCUSSION

The medullary bundle network of *C. fulva*, when viewed in transverse section (*Fig. 1*), can be divided into two fairly distinct networks, a central one of apparently random anastomoses and a peripheral one composed of groups of bundles

associated with particular leaf gaps, either along the inner face of the main meristele or as paired "radial strips" as in *C. medullaris* (Forst.) Swartz (Godwin, 1932).

The majority of the bundles which form these "radial strips" (seen in *Figure 1* as elongated sclerenchymal sheaths associated with the open leaf gaps) are derived from the central system. This system, as shown by the film sequence obtained from Segment 2 (*Fig. 1*), maintains a fairly constant number of bundles along the length of the segment with a net production of new bundles due to a surplus of branching over fusion of existing bundles. An analysis of bundle "drift" in this region (*Fig. 2*) shows that this net production and outward radial displacement of bundles is most pronounced toward the outer rim of the network, whereas the region corresponding to the center of the stem (marked by a circle in *Figs. 1* and *2)* shows almost none.

While Ogura (1972) and Lucansky (1974) report "de novo" or "independent" origins of medullary bundles in many other tree fern species, this feature was seen very infrequently in the central system of *C. fulva*, and usually in sufficient proximity to an existing bundle to suggest possible vascular continuity. However, in the peripheral system, certain bundles, when traced downwards, lose their sclerenchymal sheaths and become difficult to distinguish from the numerous mucilage ducts running through the region. Whether they arise "de novo" or as imperceptible branches from existing bundles is therefore uncertain.

The bundles of the peripheral network can be divided into three types. Type A bundles "appear" and acquire a sclerenchymal sheath in the outer extremity of a closing leaf gap (*Fig. 3*), and depart through the third leaf gap above their level of appearance (*Fig. 4*) to the innermost points of the lateral folds of the petiole trace (*Fig. 5*) after sending off a branch to the main meristele (*Figs. 6-8*). Type B bundles "appear," acquire a sheath, and drift outward to the inner face of the main meristele (*Fig. 3*). They then fuse with the type C bundles three gaps above their level of appearance (*Fig. 4*). Type C bundles arise by branching from the outer regions of the central system (*Fig. 3*), fuse with the B bundles from three leaf gaps below, and depart through the immediate leaf gap (*Fig. 4*). They then proceed to the infolding of the adaxial arc of the petiole trace (*Fig. 5*) after fusing temporarily with the main meristele (*Fig. 8*), sending a branch to it (*Figs. 6* and *8*), or temporarily fusing with the already detached "vascular plate" (*Fig. 7*).

The only points of contact between the medullary system and the main meristele are the outer edges of the leaf gap (*Figs. 6* and *8*), which, after gap closure, depart outward as the "vascular plate," and subsequently break up to form the various bundles of the adaxial arc of the petiole trace (*Fig. 5*). If the "vascular plate" detaches before gap closure, as in Gap 2 (*Fig. 7*), the C bundles then depart into the petiole without making contact with the main meristele. A similar situation is seen in Gap 3 (*Fig. 6*), where an A3 bundle sends a branch into the petiole also without making contact with the main meristele. Thus, a certain amount of variation in leaf gap anatomy is possible; however, blind endings of bundles in the leaf gap, as reported in other Cyatheaceae (Lucansky, 1974), were never seen. Nor were any bundles seen to make contact with the inner face of the main

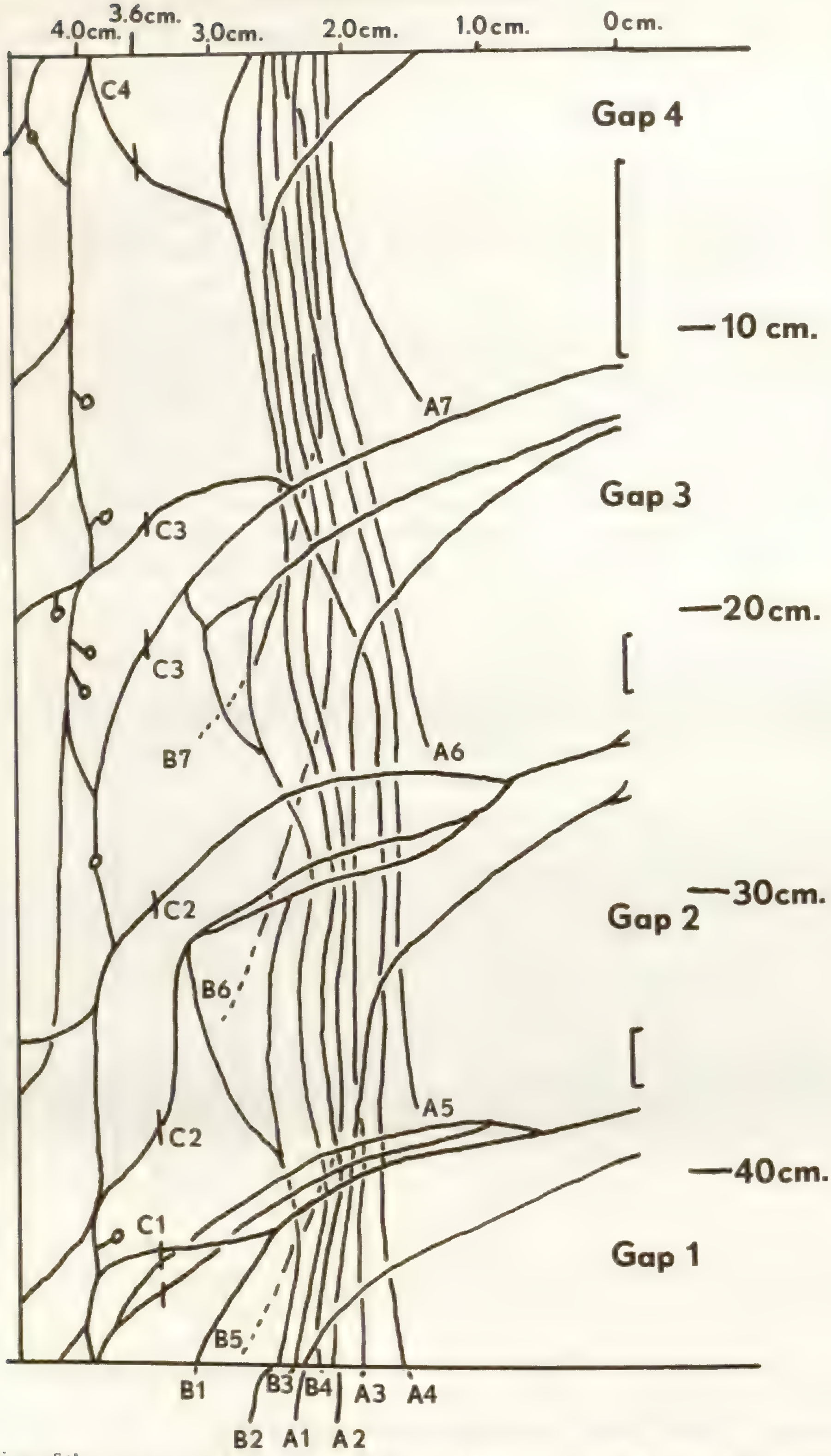


FIG. 4. Tracing of the courses of the A, B, and C bundles associated with one side of the orthostichy of leaf gaps in Segment 3. The portion to the left of centimeter 3.6 into the central zone is based on the study of Segment 1. Bundles are numbered according to the leaf gap through which they depart. Points of crossover to the adjacent orthostichy are marked by small circles.

meristele, as reported in *C. medullaris* (Godwin, 1932) and in *C. mertensiana* Copel. (Ogura, 1972).

The border between the central and peripheral systems is clearly seen in studying the film made from Segment 1 (*Fig. 1*). Associated with each orthostichy of

Fig.5

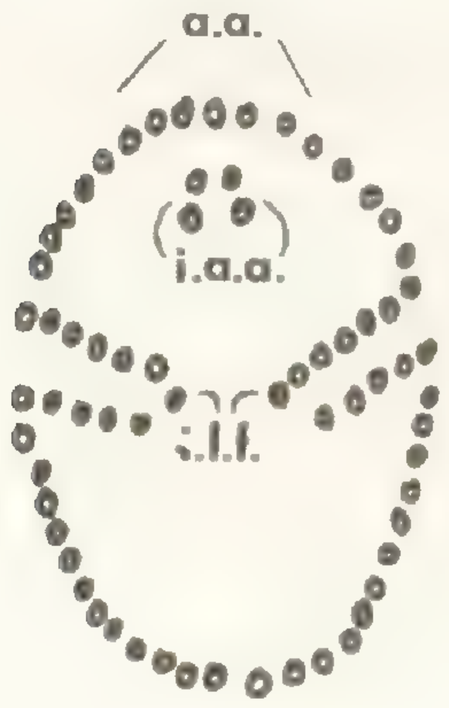


Fig.6

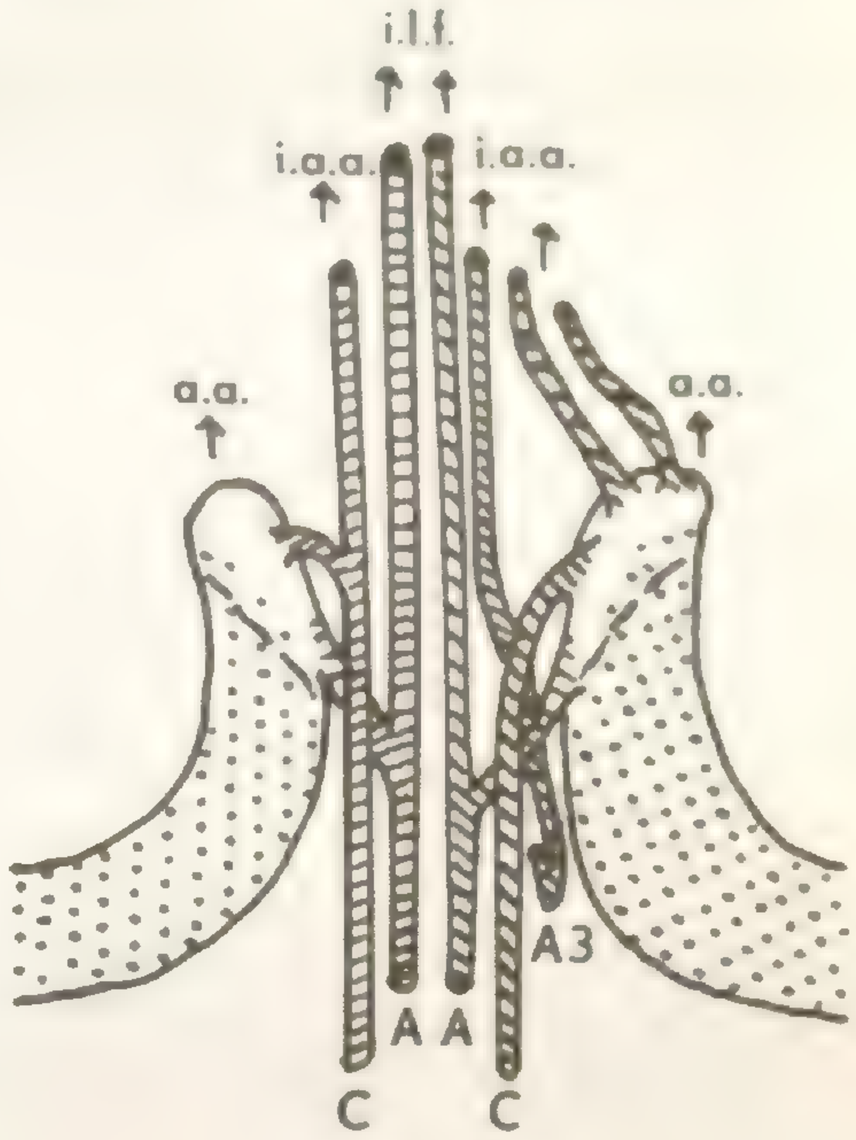


Fig.7

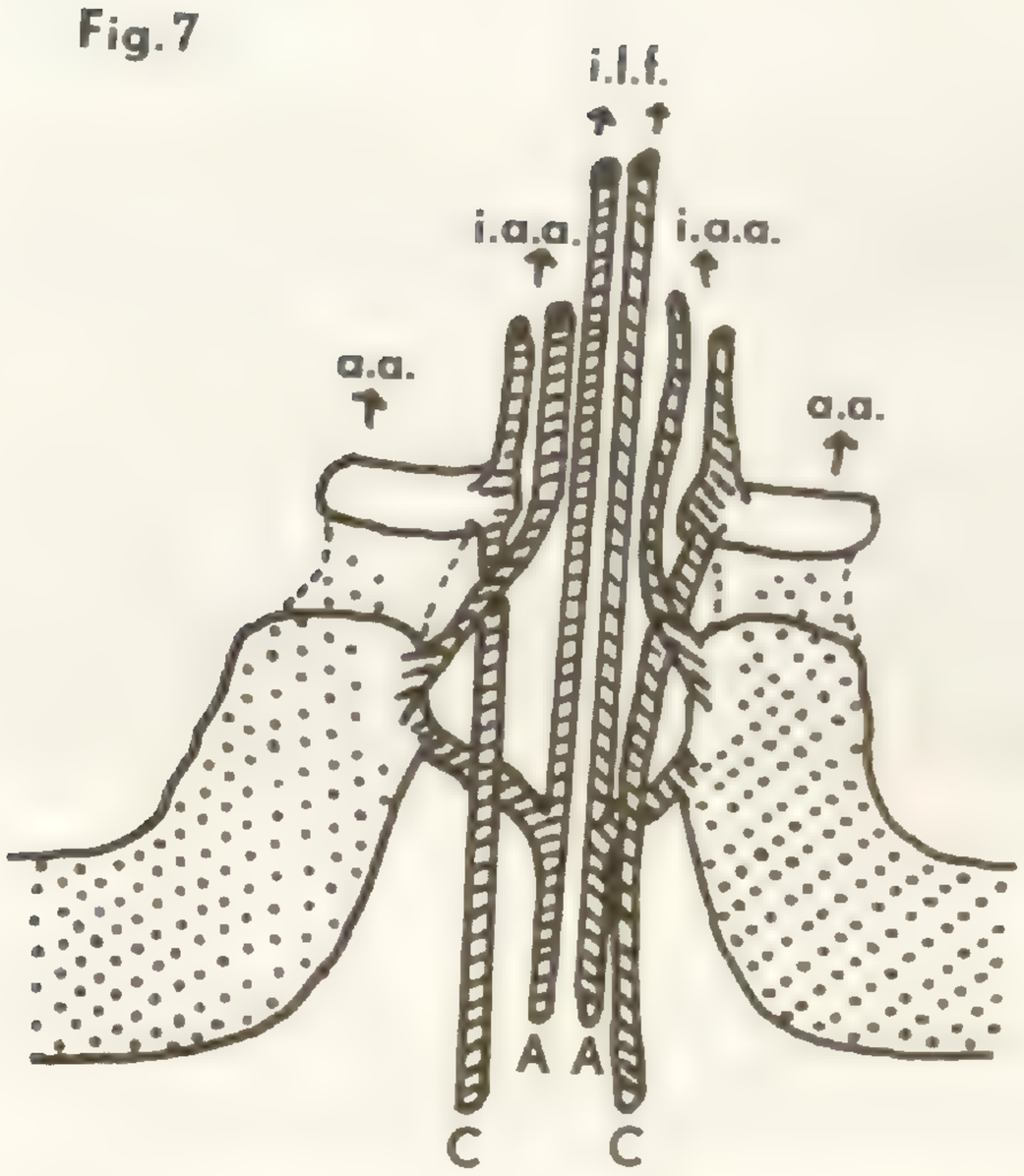


Fig.8

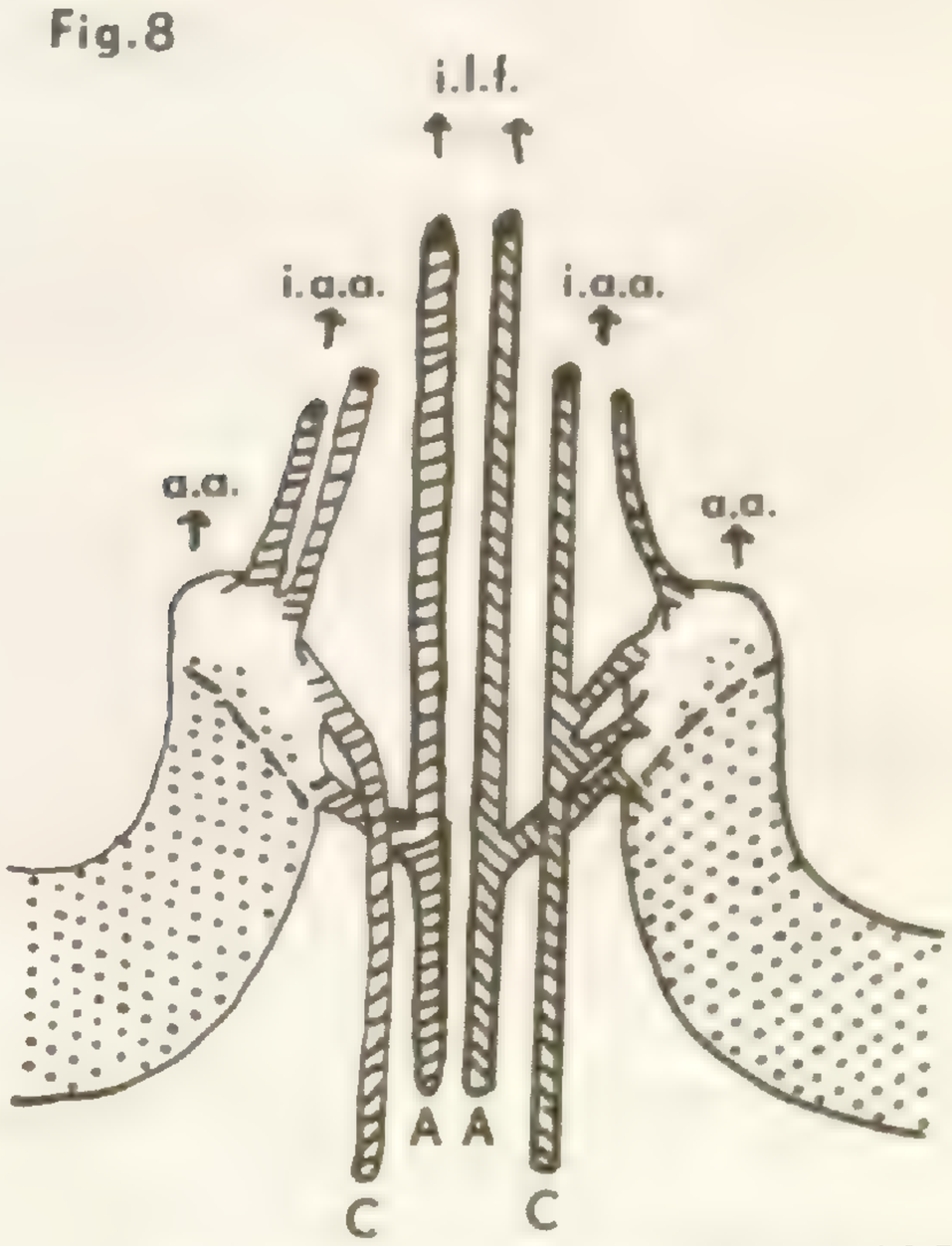


FIG. 5. Transection of the petiole trace. a.a. = adaxial arc, i.a.a. = infolding of the adaxial arc, i.l.f. = innermost points of the lateral folds. FIG. 6. Top view reconstructions of leaf gaps 3 (*Fig. 4*) showing the destinations of the bundles as marked in *Fig. 5*. Stippled areas are the main meristele, hatched areas medullary bundles and associated bundles to and from the main meristele, and the dashed lines mark off the portions of the main meristele which detach to form the vascular plate and subsequently the adaxial arc. FIG. 7. Top view reconstruction of leaf gap 2 (*Fig. 4*). FIG. 8. Top view reconstruction of leaf gap 1 (*Fig. 4*).

leaf gaps is a distinct set of A, B, and C bundles, which are always separate from those of adjacent orthostichies. While crossovers between the B and C bundles of the paired "radial strips" do occur in the peripheral region, crossovers between C bundles of adjacent orthostichies (marked by circles in *Figure 4*) occur only at the edge of the central system (marked by a line in *Figure 3*).

The close association between the medullary bundle system and the leaves lends support to the theory that the medullary system facilitates photosynthate transport into and out of the pith (Schütze, 1906). Another possible role is as a water transport system from a reservoir in the pith to the main meristele, as suggested by Tansley and Lulham (1905) in *Matonia pectinata* R. Br., which has a tricyclic solenostele. Judging, however, from the extent of contact between the medullary system and the main meristele, this role would appear to be less one of compensation for water diverted into the leaves than one of more or less direct transport into the leaves themselves. The contacts with the main stele would assume more importance once a leaf had fallen off. Unfortunately no physiological studies have been done to help clarify this matter.

The surface cinematographic method used in this study produces a more highly detailed picture of the medullary system than that possible with other methods, such as the macrotome method (Lucansky, 1974) or dissection (Godwin, 1932), in that it reveals more clearly the continuity within the central system and its relation to the peripheral system and the leaf gaps. If this method were to be used in the anatomical study of other cyatheaceous species possessing medullary bundles, similar continuity might become apparent. In addition, examination of juvenile plants of *C. fulva* and of serial sections of the stem apex itself could serve to supplement the knowledge of the ontogeny and function of the medullary system.

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Asplenium azoricum and Other Ferns of the A. trichomanes Group from the Azores

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Asplenium trichomanes L. is an aggregate species of world-wide distribution. Diploid, tetraploid, and hexaploid (in Australia and New Zealand) cytotypes are known, the first two of which are polymorphic. Only a few of these forms have botanical names. We use here the nomenclature and typification of Lovis (1964). Löve and Kjellqvist (1972) and Löve and Löve (1974) suggested assigning specific rank to the diploid and tetraploid cytotypes, following Rothmaler (1966, p. 5) and Soó in Fuchs (1963). In principle this is acceptable, but it is very impractical because there are many cases in which even specialists are unable to differentiate between the cytotypes with confidence when dealing with herbarium material.

According to Carvalho e Vasconcellos (1968), both the diploid *A. trichomanes* subsp. *trichomanes (sensu* Lovis, 1964) and the tetraploid subsp. *quadrivalens* D. E. Meyer (1962) are assumed to grow in the Azores, but Pinto da Silva in Palhinha (1966) was more cautious. He quoted Lovis' opinion of that time: "However, the only form of *A. trichomanes* from Azores yet studied alive is a peculiar form, and requires more study before it can be given an accurate taxonomic treatment." Franco (1971, p. 23) did not differentiate between the subspecies. Wilmanns and Rasbach (1973, p. 326) stated that most specimens differ from Central European *A. trichomanes* subsp. *quadrivalens* by brightness, longer pinnae, and stronger teeth. Sjögren (1973, p. 85), Eriksson et al. (1974, p. 1), and Pinto da Silva and Pinto da Silva (1974, p. 14) reported only subsp. *quadrivalens* for the Azores.

Of related species in the Azores, all authors mention *A. monanthes* L. The following also report *A. anceps* Lowe ex Hook. & Grev.: Bolle (1866, p. 215), Milde (1867, p. 64, *sub A. trichomanes* var. *anceps* f. *azorica*), Drouet (1866, p. 131), Sauer (1880, p. 43), Trelease (1897, p. 172, *sub A. trichomanes* var. *anceps* f. *azorica),* Palhinha (1943) and Benl and Sventenius (1970, p. 447). We suspect that all these reports are wrong because of confusion with *A. azoricum.*

We have not seen the specimen that Bolle quoted, but he stated that the only specimen from the Azores he had seen, which was collected by A. Braun, showed a more pronounced dentation at the tip and acroscopic side of the pinnae. This is typical of *A. azoricum,* and we suspect that his specimen was indeed that species. Milde's type and sole specimen is *A. azoricum.* Sauer did not mention any specimens, but cited only "Azores." We have seen two specimens of Drouet (BM), 11 out of the 19 specimens cited by Trelease, and all five quoted by Palhinha. None is *A. anceps.* Benl and Sventenius based their record of *A. anceps* on the literature mentioned above (Benl, in litt.). So far we have been unable to detect any specimen of *A. anceps* from the Azores in any herbarium.

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FIG. 1. Photocopies of *Asplenium* frond silhouettes, × 1. A. = *A. monanthes* (Azores, cult., *TR-3355*). B = *A. trichomanes* subsp. *quadrivalens* (Azores, cult., *TR-3497*). C = *A. anceps* (Madeira, wild collection, *TR-2559*). D= *A. heterochroum*, 4x (Florida, cult., *TR-3403*). E =*A. heterochroum*, 4x (Bermuda, cult., *TR-3952-A*). F = *A. azoricum* (Azores, cult., *TR-3335-2*). (J. v. Euw photos)

MATERIAL AND METHODS

Fronds with ripe spores (and also living plants in a few cases) were collected and field notes and photographs were taken during a visit of H. and K. Rasbach and H. L. and T. Reichstein to four of the nine inhabited islands of the Azores (Santa Maria, São Miguel, Faial, and Pico) between 19 April and 13 May 1973. In Basel, gametophytes were raised from spores on agar and then were transplanted

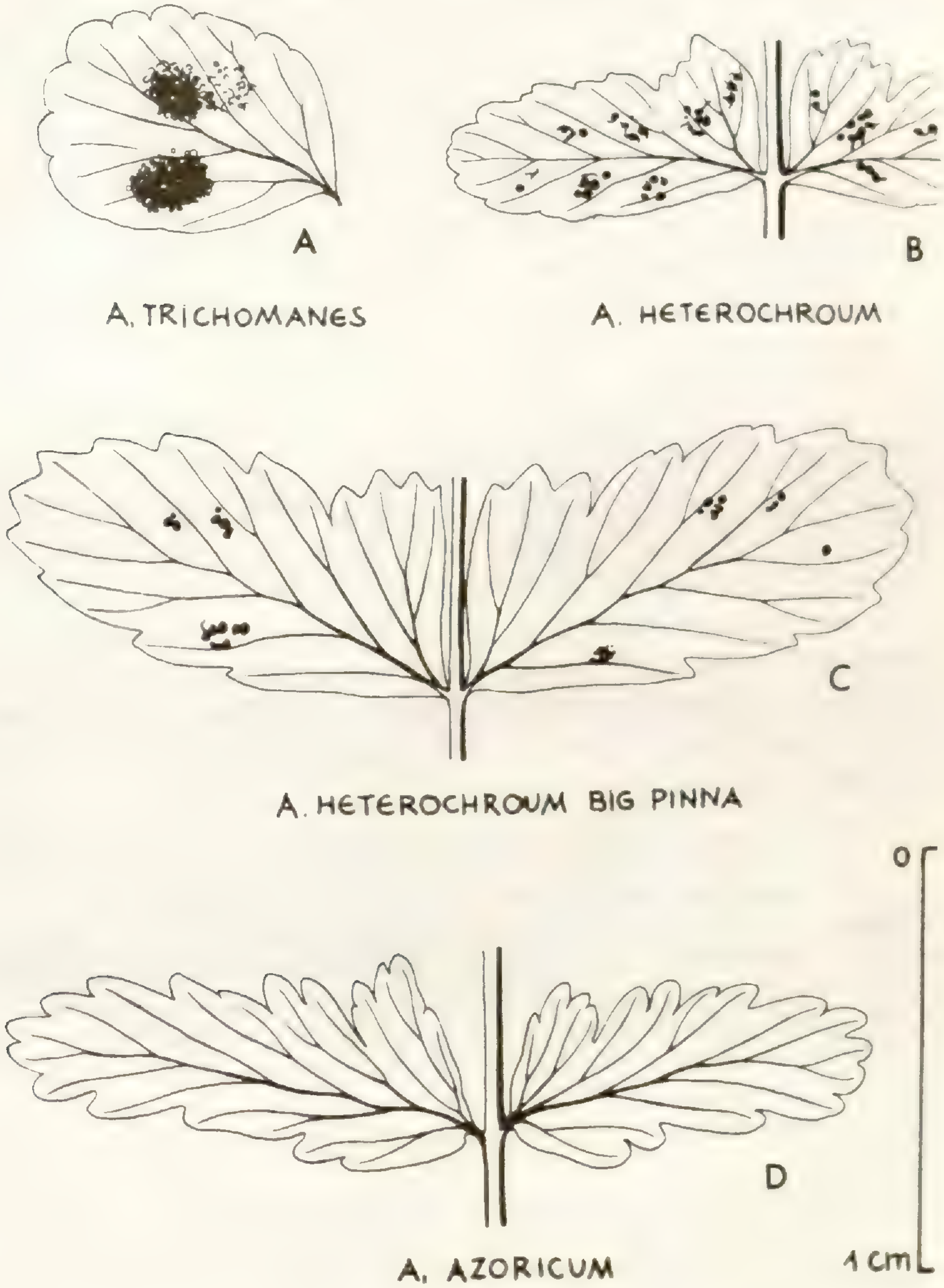

FIG. 2. Median *Asplenium* pinnae cleared in 70% chloral hydrate. × 5. The sori are lost in this procedure. A = *A. trichomanes* subsp. *quadrivalens* (Azores, cult., *TR-3466*). B and C = *A. heterochroum* (Florida, cult. from spores of *Wagner 62087*, *TR-3403*). D = *A. azoricum* (Azores, cult., *TR-3336*). (Drawn by R. Hirzel)

on soil (for details see Reichstein et al., 1973), but in Leeds spores were germinated on soil (see Lovis, 1968). In Basel, developing sporophytes were grown in pots in a cool greenhouse (minimum temperature 2°C) during the winter. In summer, the plants were kept outside in half-shade. For cytological work, fronds with immature sporangia were fixed in a 1:3 glacial acetic acid:absolute ethanol solution, which was replaced with fresh fixative after about 24 hours. Some material was fixed in the field; other material was fixed from cultivated plants in Basel or Leeds. Preparations of meiosis were made following Manton (1950, pp. 293–299). Root tips were pretreated in 0.1% aqueous colchicine solution for about 8 hrs at 4–6°C. Cytological results are illustrated here only for taxa not previously illustrated. Spores to be measured were embedded in balsam; only epispore length was measured.

Living material of the tetraploid (*Wagner 62057*, $n=72$) and hexaploid (*Wagner 62055-5*, $n=108$) cytotypes of *A. heterochroum* Kunze from Florida was raised from spores of cytologically checked plants kindly provided to Lovis by Wagner in July, 1963. The former is from the fern grottoes at Pineola, near Istachatta, Citrus–Hernando County; the latter is from 2.95 miles NW of the Santa Fe River just N of Rte. 27, Columbia County. Material of *A. heterochroum* from Bermuda, which was proved to be tetraploid by Lovis, was kindly collected by Fraser-Jenkins. The vouchers are *TR-3950* (separated on arrival into 13 pieces labelled A–M) from 0.5 km E of Leamington Caves, Hamilton Parish and *TR-3952* (separated on arrival into 7 pieces labelled A–G) from calcareous rocks on the Ocean View golf course, Tucker's Town. After splitting, the plants had only very little or no roots at all and were treated like cuttings, covered with plastic cups for about eight weeks until new fronds appeared, the cups gradually lifted, the plants kept without cups in the greenhouse for 4–6 weeks, and finally put outdoors in pots during the summer. All the plants developed well and became fertile by the end of 1976. *TR-3950M* was found to have n=72.

KEY TO THE ASPLENIUM TRICHOMANES GROUP IN THE AZORES

1. Fertile pinnae strongly asymmetrical, with a very narrow, basiscopic side (*Figs. 1A, 2A*); only one sorus along the costa (*Fig. 3B*). Spores ca. (30)39–42(45) μm long.....1. *A. monanthes*
1. Fertile pinnae approximately symmetrical, with the basiscopic side as large as or only a little smaller than the acroscopic side (*Figs. 1B, C, F*); usually several sori along the costa, these sometimes appearing confluent at maturity (*Figs. 3A, D, E*).
   2. Rachis with two lateral wings plus a distinct, third wing 0.1–0.3 mm wide on the abaxial side (*Figs. 4D, E*). Spores very small, (21)28–30(32) μm long.....3. *A. anceps*
   2. Rachis with only two lateral, adaxial wings borne along the lines of insertion of the pinnae (*Figs. 4B, F*).
      3. Pinnae apple-green, with a dull surface; median pinnae suborbicular-oval, often cuneate at the base, but not auriculate, less than twice as long as wide, often nearly symmetrical, the costa inconspicuous, the lateral veins often forked (*Figs. 1B, 2A*); spores (27)36–39(41) μm long.....2. *A. trichomanes* subsp. *quadrivalens*
      3. Pinnae bright bottle-green, with a glossy surface; lower pinnae usually distinctly biauriculate; median pinnae more than twice as long as wide, usually somewhat asymmetrical with the acroscopic side a little wider than the basiscopic side, the costa pronounced, the veins usually simple, but those of the auricle often forked (*Figs. 1F, 2D*); spores (24)30-36(39) μm long.
      4. *A. azoricum*

1. Asplenium monanthes L. Mant. Plant. 130. 1769.

This species is widespread, being reported from Mexico to Chile, Jamaica, Hispaniola, much of Africa, Madagascar, the Hawaiian Islands, the Macaronesian Atlantic islands (excluding the Cape Verde islands), and Tristan da Cunha. In the Azores we have seen this species only on São Miguel and on Pico (*Fig. 7*), but according to Palhinha (1966) and Eriksson et al. (1974), it grows on six islands and is absent only from Santa Maria, Graciosa, and Corvo. Sjögren (1973) confirms its presence on São Miguel, Terceira, and Pico. Specimens from Madeira (Manton, 1950, p. 195; Manton in Alston, 1959, p. 80) and from Tristan (Manton & Vida, 1968, p. 364) were triploid and apomictic. The same was found for a plant (*TR-3355*) raised from spores from Sierra da Tronqueira on São Miguel (10 Apr 1972, *R. Gumprecht et al.)* which had n=ca. 108 and $2n$=ca. 108, according to Vida (*in litt*. 24 May and 1 Sept 1975).

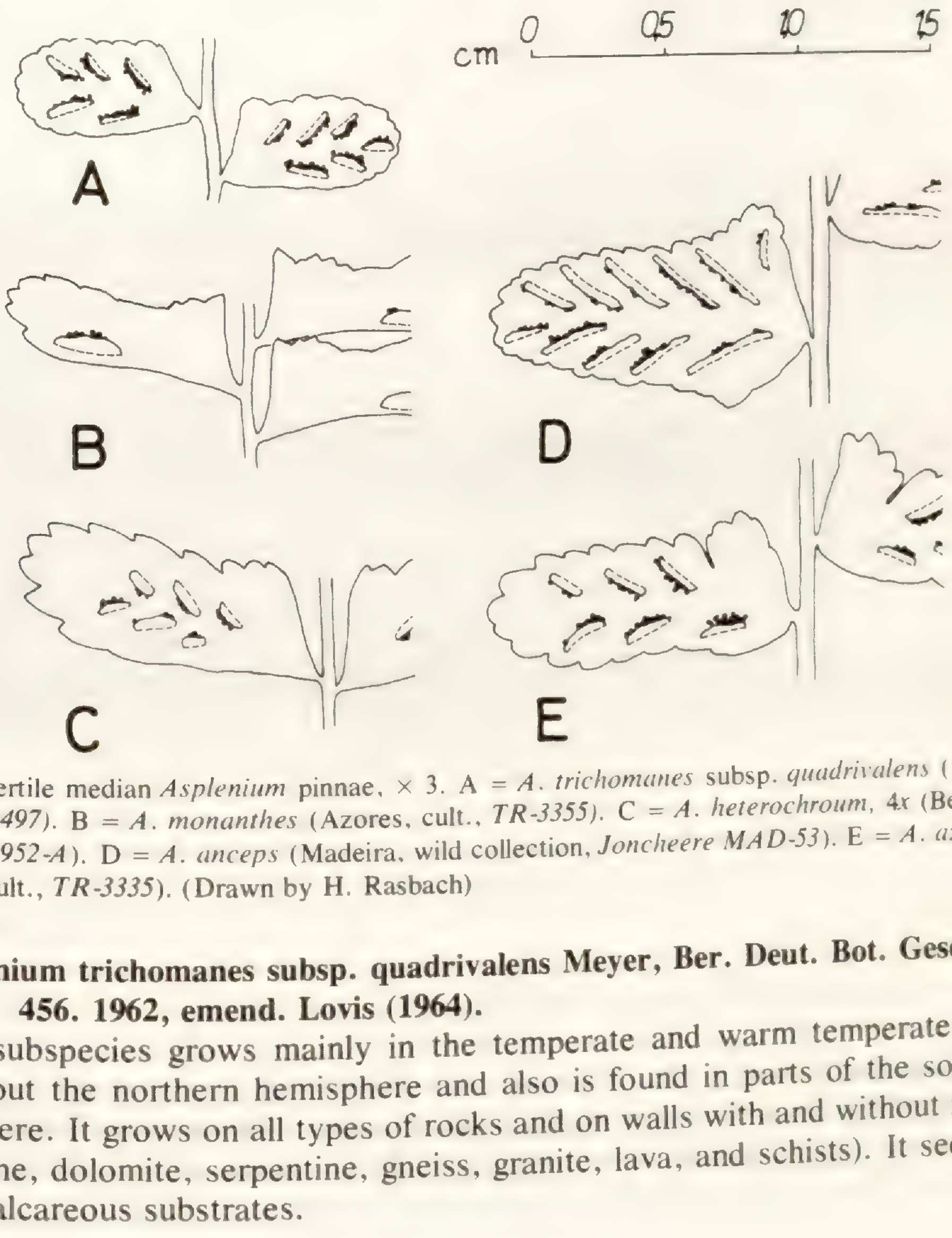

FIG. 3. Fertile median *Asplenium* pinnae, × 3. A = *A. trichomanes* subsp. *quadrivalens* (Azores, cult., *TR-3497*). B = *A. monanthes* (Azores, cult., *TR-3355*). C = *A. heterochroum*, 4x (Bermuda, cult., *TR-3952-A*). D = *A. anceps* (Madeira, wild collection, *Joncheere MAD-53*). E = *A. azoricum* (Azores, cult., *TR-3335*). (Drawn by H. Rasbach)

2. Asplenium trichomanes subsp. quadrivalens Meyer, Ber. Deut. Bot. Gesell. 74: 456. 1962, emend. Lovis (1964).

This subspecies grows mainly in the temperate and warm temperate zones throughout the northern hemisphere and also is found in parts of the southern hemisphere. It grows on all types of rocks and on walls with and without mortar (limestone, dolomite, serpentine, gneiss, granite, lava, and schists). It seems to prefer calcareous substrates.

We found *A. trichomanes* subsp. *quadrivalens* on three of the four islands we visited, often locally abundant (*Fig. 6*), occasionally on rock (basalt, lava), although more often on walls with and without mortar, in all possible exposures, but preferentially in open situations, sometimes southern exposures in full sun. Many plants were well developed and recognizable by their morphology, since they corresponded to cytologically checked specimens of this subspecies from Europe, the Canary Islands, and Madeira. We selected a few plants for spore measurements which were not distinctive enough in the field to exclude the possibility that they might be the diploid subsp. *trichomanes (sensu* Lovis, 1964). A particularly suspicious plant (*TR-3466)* was taken into cultivation. A cytological check showed it to be tetraploid, and after some months it developed the normal characteristics of subsp. *quadrivalens*.

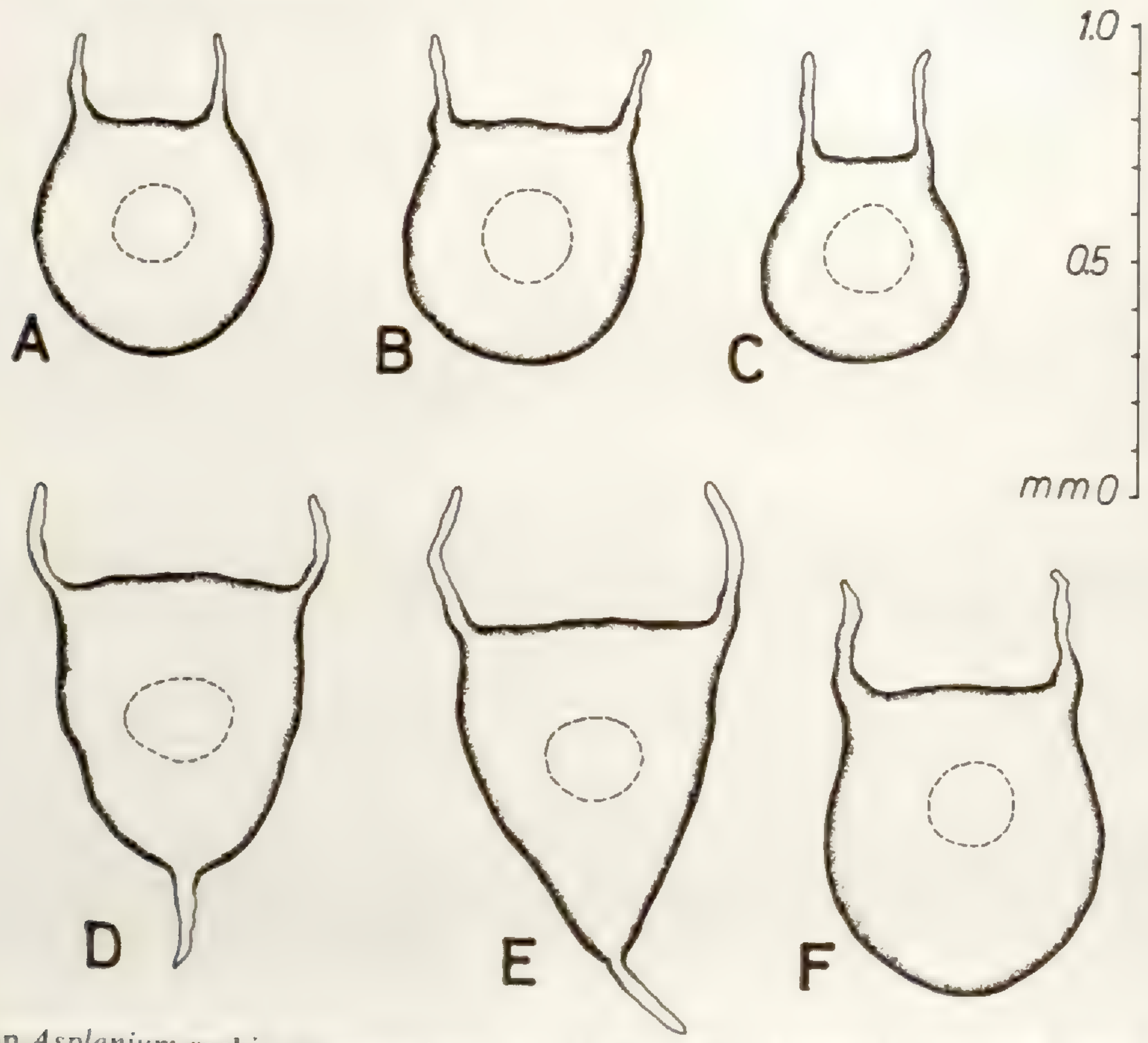

FIG. 4. Median *Asplenium* rachis cross-sections, ×5. Frond length follows collection data. A = *A. monanthes* (Azores, *RAS-10.4.72*, 14 cm). B = *A. trichomanes* subsp. *quadrivalens* (Azores, *RAS-17.4.72*, 13 cm). C = *A. heterochroum* (Bermuda, *TR-3952*, 16 cm). D = *A. anceps* (Madeira, *TR-2559*, 13 cm). E = *A. anceps* (Azores, *RAS-1*, 8 cm). F = *A. azoricum* (Azores, *TR-3335*, 14 cm). (Drawn by H. Rasbach)

The diploid subsp. *trichomanes* has a similar but slightly more northern distribution than subsp. *quadrivalens* and prefers cooler situations. However, it never grows on limestone or dolomite, but is sometimes found on serpentine, although it occurs more often on gneiss, granite, and other silicate rocks or walls. The Azores appear to offer ideal habitats for this subspecies, but so far we have not found it. We suspect that it is not there nor on the other Macaronesian islands.

3. Asplenium anceps Lowe ex Hook. & Grev. Icon. Fil. 2: t. 195. 1830–31.

Asplenium anceps Solander ms. (BM; see Britten, 1904, p. 199).
Asplenium anceps R. Br. ex L. von Buch, Phys. Beschr. Canar. Ins. 189. 1825, *nom. nud.*
Asplenium anceps Lowe, Trans. Cambridge Phil. Soc. **4:** 8. June 1831.

TYPE: "Madeira, *Fr. Masson 1778*" [in Banks' hand] (BM-Hb. Banks).

The foregoing synonymy is given after a careful search at BM in 1975. The nature of the plant intended by Lowe and by Hooker and Greville is not in doubt. Their two publications were almost simultaneous; possibly nobody knows which appeared first. It is clear from their text that Hooker and Greville did not intend to anticipate Lowe. In the absence of definite publication dates, we prefer the citation Lowe ex Hook. & Grev. because when so attributed, the identity of the plant is unambiguous. For additional synonyms, see Benl and Sventenius (1970, p. 447).

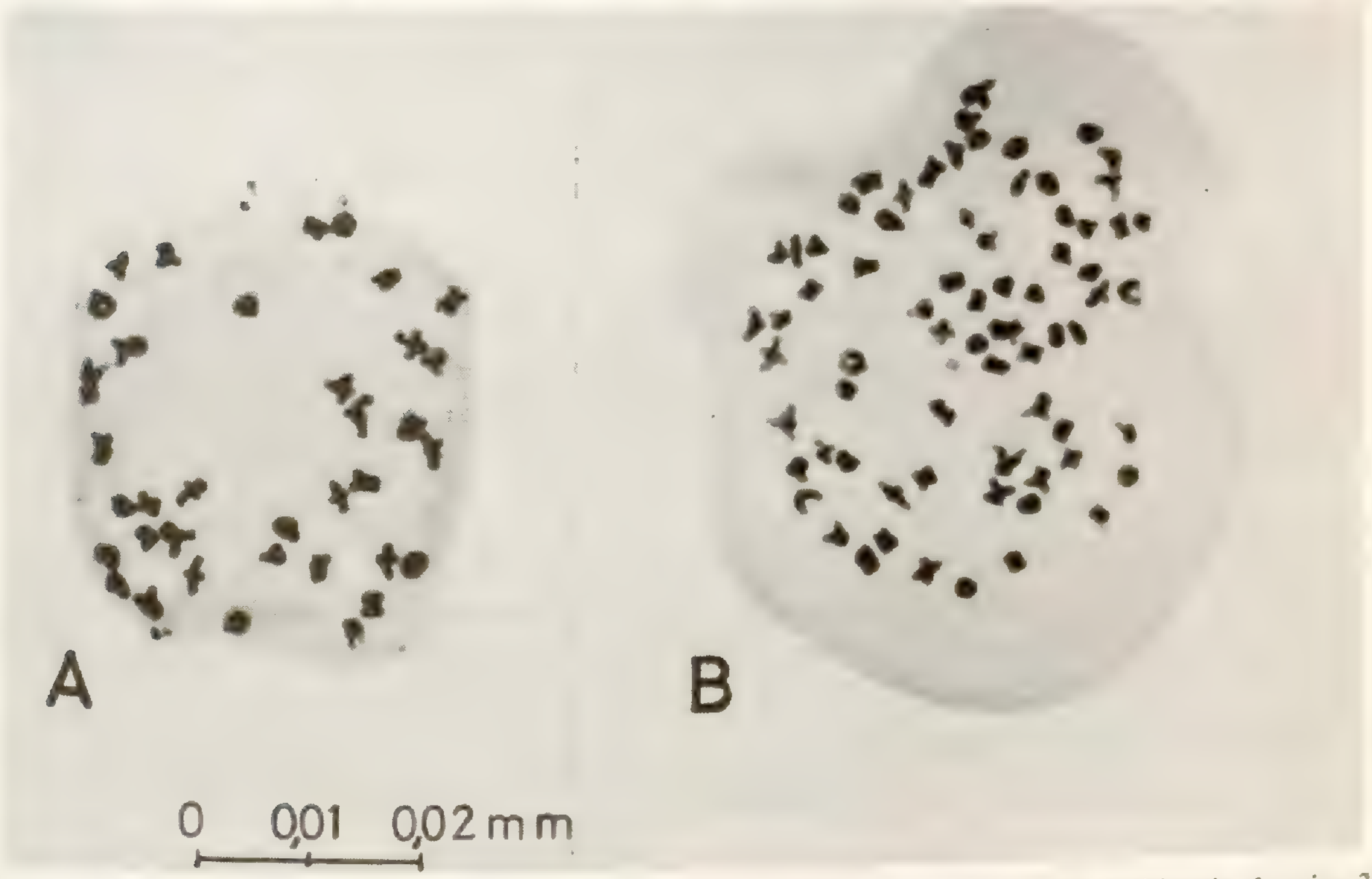

FIG. 5. Spore mother cells of *Asplenium* at meiosis, × 1000. A = *A. anceps* at diakinesis showing 36 pairs (Azores, *RAS-1*). B = *A. azoricum* at diakinesis showing 72 pairs (Santa Maria, Azores, cult. J. D. Lovis from spores from *B.F.C. Sennit* in 1953, BM). Progeny of *TR-3336* cultivated in Basel also gave $n = 72$. (Prep. and photos by J. D. Lovis)

This species is sometimes treated as a subspecies or variety of *A. trichomanes* and is often confused with *A. trichomanes* subsp. *quadrivalens*. Plants raised from spores collected at the Levada do Ribeira Frio, Madeira, ca. 850 m altitude (Nov 1958, *G. J. de Joncheere*) sown in Basel in January, 1966 giving copious progeny (*TR-1642*), were diploid according to Lovis, who was quoted by Meyer (1969, p. 225). Several other Madeiran collections also have proved to be diploid (Lovis, unpubl.). On cytological grounds alone, *A. anceps* therefore cannot be accepted as a variety of subsp. *quadrivalens*. *Asplenium anceps* is easily recognized by the third wing on the abaxial side of the rachis (*Fig. 4*), which is not present in the other Macaronesian members of the group. However, it possesses a suite of

distinctive characters, namely the third rachis wing, pinnae regularly arranged and squarely inserted, pinnae regular in shape and about twice as long as broad, sori numerous and evenly distributed, and adaxial surface of the pinnae appearing dark and glossy. The regularly arranged and squarely inserted pinnae that are dark and glossy above give the plant a characteristic, elegant appearance. Only the first and last character is shared with *A. azoricum*.

Asplenium anceps is relatively common in Madeira (Lowe, 1831, p. 8; Benl, 1971; unpubl. observations by G. J. de Joncheere in 1958 and by de Joncheere, Lovis & Reichstein in 1969), but was already rare in the Canary Islands in the 19th Century (Bolle, 1866, p. 214). It was reported more recently by Benl and Sventenius (1970, pp. 446–447) and by Page (1971), particularly for La Palma. Although it is endemic to the Macaronesian islands, it is closely related to the Japanese species *A. tripteropus* Nakai (=*A. anceps* var. *proliferum* Nakai) and, according to Christenser. (1934, p. 38), to *A. regulare* Swartz from Brazil. The Japanese plant often produces proliferous buds on the upper part of the rachis, which never occur in *A. anceps s. str. Asplenium tripteropus* also differs in possessing prostrate fronds with dull, gray-green pinnae of thin texture, unlike the suberect fronds with glossy, dark green pinnae of *A. anceps*. We do not agree with Löve et al. (1977, p. 257), who treat *A. anceps* as a synonym of *A. trichomanes* subsp. *tripteropus*, or with their treatment of *A. tripteropus* as a subspecies of *A. trichomanes*. We prefer to follow Tagawa (1967) and other Japanese experts who recognize and accept *A. trichomanes* and *A. tripteropus* in their own country.

H. and K. Rasbach found *A. anceps* on Pico on 10 May 1973 as a rarity. They found only two plants on the northwest slope of Mount Pico at ca. 825 m altitude, where they were growing in a north-exposed wall composed of coarse, basaltic blocks without mortar (*RAS-1* and *RAS-2*). The plants were growing with *Hymenophyllum wilsonii* Hook., *Elaphoglossum paleaceum* (Hook. & Grev.) Sledge, and many mosses and lichens. This indicates that the site must have a high humidity throughout the year. A frond of *RAS-1* fixed in the field showed $n=36$ (*Fig. 5A*).

4. Asplenium azoricum Lovis, Rasbach & Reichstein, sp. nov.

A. trichomanes var. *anceps* f. *azorica* Milde, Fil. Eur. Atlant. 64. 1867. LECTOTYPE: "ad muros, insul Fayal," Azores, *Hochstetter Pl. Azor. 174* (BM; possible isotype FR labelled "Flores" not in Milde's hand).

Planta *Asplenio heterochroo* similis sed in superficie statu vivo magis nitente, textura firmiore, petiolo rachique crassioribus et rigidioribus, pinnis partis basalis tertiae vel medii inferiore laminae plerumque utrinque auriculatis, et in soris longioribus differt.

TYPE: Cultivated at Basel from spores from near Feteira Pequena, São Miguel, Azores, ca. 100 m alt, *Reichstein TR-3335* (BM; isotypes G, K, P, US). The wild material was collected by R. Gumprecht, H. & K. Rasbach, and O. Wilmanns on 8 Apr 1972.

PARATYPES (all from the Azores):

SANTA MARIA: *H. Drouet* (BM, two specimens *sub A. anceps*); 26 Jun 1906, *W. Trelease 1187a* (MO, *sub A. trichomanes*); *B. F. C. Sennit 71* in 1953 (BM, *sub A. trichomanes*); Faneca, 150 m alt, 3

May 1972, *B. Gonçalves 4017a* (BM, *sub A. trichomanes*); Pico Alto, 580 m alt, 23 Apr 1972, *B. Gonçalves 3885* (BM, *sub A. trichomanes*); Walls along road from Vila do Porto to Almagreira and Feteiras de S. Pedro, 180–200 m alt; plentiful, further isolated plants scattered to Pico Alto, 580 m alt, 19 Apr and 11 May 1973, *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Reichstein *TR-3456, TR-3539*).

SÃO MIGUEL: *T. C. Hunt* in 1845 (BM, *sub A. anceps*); Lagoa das Furnas, 26 Aug 1894, *W. Trelease 1187* (MO, *sub A. trichomanes*); Charco da Madeira, Apr 1898, *B. T. Carreiro 585* (COI, *sub A. anceps*, MO, *sub A. trichomanes*); Vila Franca, 5 Apr 1972, *R. Gumprecht, H. & K. Rasbach & O. Wilmanns* (Hb. Reichstein *TR-3353*); Walls between Livramento and Ribeira Grande, ca. 140 m alt, 23 and 25 Apr 1973, *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Reichstein *TR-3476, TR-3493*); Walls and rocks along road between Ponta Delgada and Ribeira Grande, ca. 150–200 m alt, 5 Apr 1972, *R. Gumprecht, H. & K. Rasbach & O. Wilmanns* (Hb. Reichstein *TR-3336*), *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Reichstein *TR-3452, TR-3495, TR-3521*); N slope of Pico do Carvão, ca. 650 m alt, 25 Apr 1973, *H. & K. Rasbach & H.L. & T. Reichstein* (Hb. Reichstein *TR-3487*).

TERCEIRA: Angra do Heroismo, *E. A. R. Abreu 22* in 1878 (COI, *sub A. anceps*); 5 Jul 1894, *W. Trelease 1184* (MO, *sub A. trichomanes*); Caldeira da Guilhermo Moniz in the center of the island, crevices of lava rock by road, locally frequent, ca. 400 m alt, 25 Jul 1976, *K. U. Kramer 5700* (Z).

GRACIOSA: Folga, 18 Aug 1894, *W. Trelease 1182* (MO, *sub A. trichomanes*); Caldeira, 150 m alt, 8 Jul 1971, *G. Gonçalves 3059* (BM, *sub A. trichomanes*).

SÃO JORGE: Jul 1903, *B. T. Carreiro 586B* (COI, *sub A. anceps*); Fajã Grande, *Palhinha 43697* (LISU, *sub A. anceps*); Toledo, 600 m alt, 7 Sep 1971, *B. Gonçalves 3638* (BM, *sub A. trichomanes*).

PICO: São Roque Fonte, ca. 200 m alt, 5 Aug 1971, *B. Gonçalves 3355* (BM, *sub A. trichomanes*); NW of São Roque do Pico, 200 m alt, 10 May 1973, *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Rasbach).

FAIAL: 19 Jul 1894, *C. S. Brown 340* (COI, MO, US, all *sub A. trichomanes*); Walls along road near Lombega, NW of Castelo Branco, ca. 200 m alt, 6 May 1973, *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Reichstein *TR-3523*); Walls in Praia do Norte, ca. 300 m alt, 9 May 1973, *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Rasbach); Cabeco do Fogo, 500 m alt, 15 Jan 1963, *B. Gonçalves 829* (BM, *sub A. trichomanes*); N of Capelo, ca. 200 m alt, 6 May 1973, *H. & K. Rasbach & H. L. & T. Reichstein* (Hb. Reichstein *TR-3524*).

FLORES: 12 Aug 1894, *W. Trelease 1181* (MO, *sub A. trichomanes*); Fajã Grande Coada, stone wall, 200 m alt, 2 Jul 1967, *C. M. Ward 26* (BM, *sub A. trichomanes*); Lajes Boca da Beleia, stone wall, 350 m alt, 14 Jul 1967, *C. M. Ward 37* (BM, *sub A. trichomanes*).

CORVO: *W. Trelease 1179* in 1894 (MO, *sub A. trichomanes*); Horta Velhas, 400 m alt, 8 Jun 1971, *B. Gonçalves 2580* (BM, *sub A. trichomanes*).

In the following description, the characters distinguishing *A. azoricum* from *A. heterochroum* are in italics.

Rhizome short, erect, the apex covered with scales, the fronds borne in a tuft, up to ca. 10–15(20) per plant. Stipes short, 0.5–3 cm long, *ca. 0.5–1.2(2) mm thick*, covered with scales at the base but glabrous above. Rachises glabrous, *stiff, in larger fronds brittle*, dark chestnut brown, bordered on each side with a wing ca. 0.1–0.2 mm wide. Rhizome and stipe base scales ca. (3)5(8) mm long, clathrate, light brown with a dark central stripe. Fertile fronds 3–20(32) cm long, 10–25(35) mm wide, elongate-lanceolate-subparallel in outline, widest near the middle, with 10–25(30) pairs of subsessile or short-petiolulate (ca. 0.5 mm), opposite to partly alternate, oblong-ovate lateral pinnae and often a tri-penta-partite terminal pinna; longest pinnae ca. 4–15 mm long, ca. 1.5–5 mm wide in the middle, usually acroscopically auriculate at the base, *pinnae in the lower third to half of the frond often also auriculate on the basiscopic side, these pinnae biauriculate*; upper auricle with 2–4 teeth, sometimes completely free; pinnae slightly asymmetrical, but in the widest part of the non-auriculate sector *the acroscopic portion only ca. 1.2 times wider than the basiscopic*, glabrous on both sides, *the adaxial side in living*

material bright, glossy, dark green; pinna margins dentate with incisions 0.5–1 mm deep subparallel to the midrib, the teeth ca. 0.5–1(2) mm wide, *rounded or obtusely pointed*, ± directed towards the pinna apex; veins in the auricle usually forked, but in the main part of the pinna predominantly simple, prominent on the

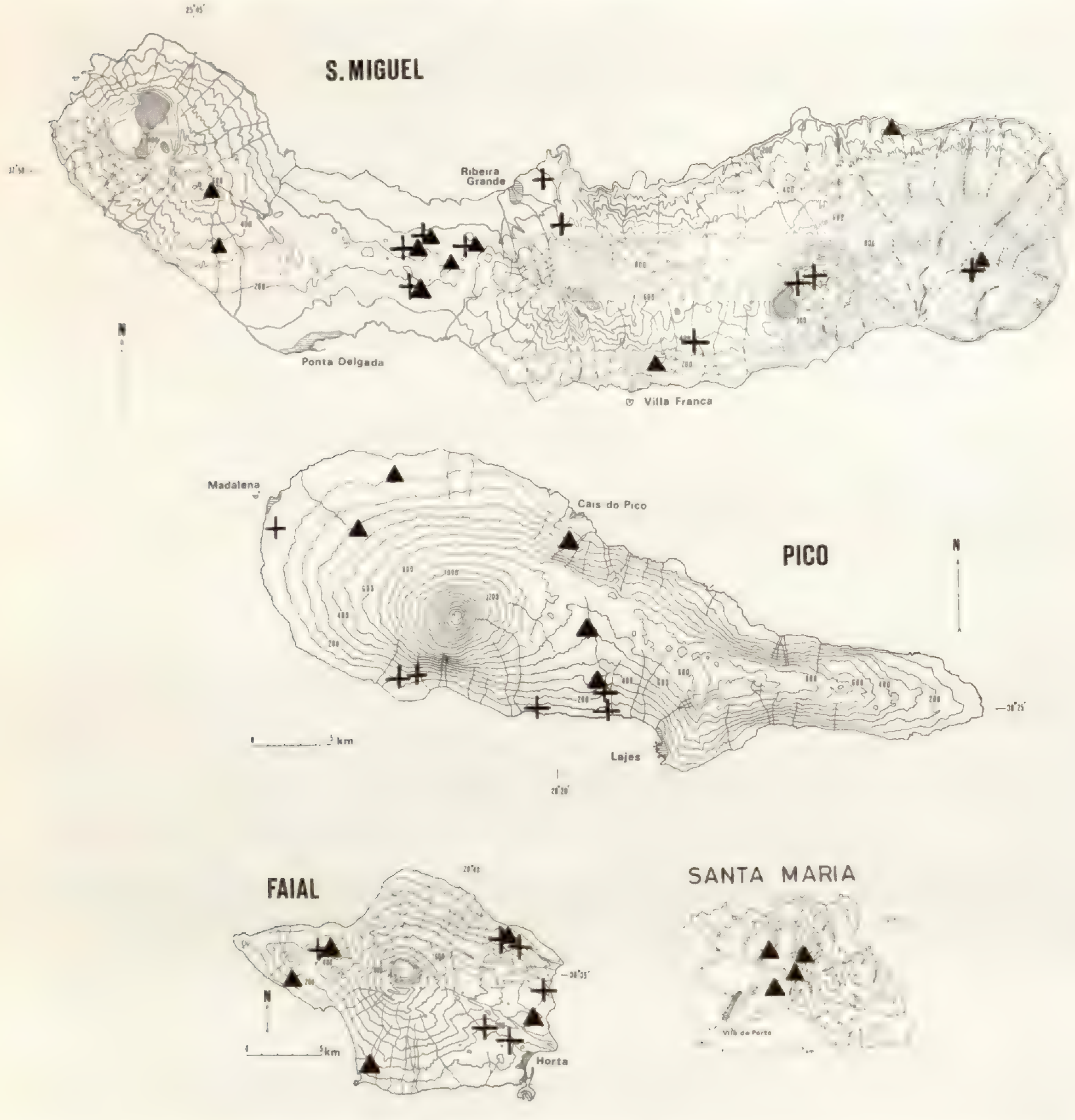

FIG. 6. ▲ = *Asplenium azoricum* and + = *A. trichomanes* subsp. *quadrivalens* as seen on the four islands in 1973.

pinna surface; sori (1)2–4(5) pairs *2–4(5) mm long, at their base close to the costa and nearly parallel to it, turning outward distally*. Spores with an epispore, (24)29–36(39) μm long, covered with a brown perispore, this irregularly protruding up to ca. 6(10) μm. Chromosome number $n=72$, $2n=144$, sexual, with 64 spores per sporangium (*Fig. 5B*).

Asplenium azoricum shows great similarity to *A. heterochroum* Kunze. We have examined an isotype of the latter species from the Embarcadero del Canimar, Cuba (*Poeppig* in 1832, B) which illustrates this. The similarity of *A. azoricum* to *A. heterochroum*, particularly in herbarium material, is so close that at one time we intended to classify *A. azoricum* as a subspecies of *A. heterochroum*. Comparison of living material made the differences more clearly visible. The two species are also well separated geographically. We therefore think that it is more appropriate to treat *A. azoricum* as a separate species. We hope that experimental hybridization will allow the true degree of relationship of these two and other taxa of the group to be known.

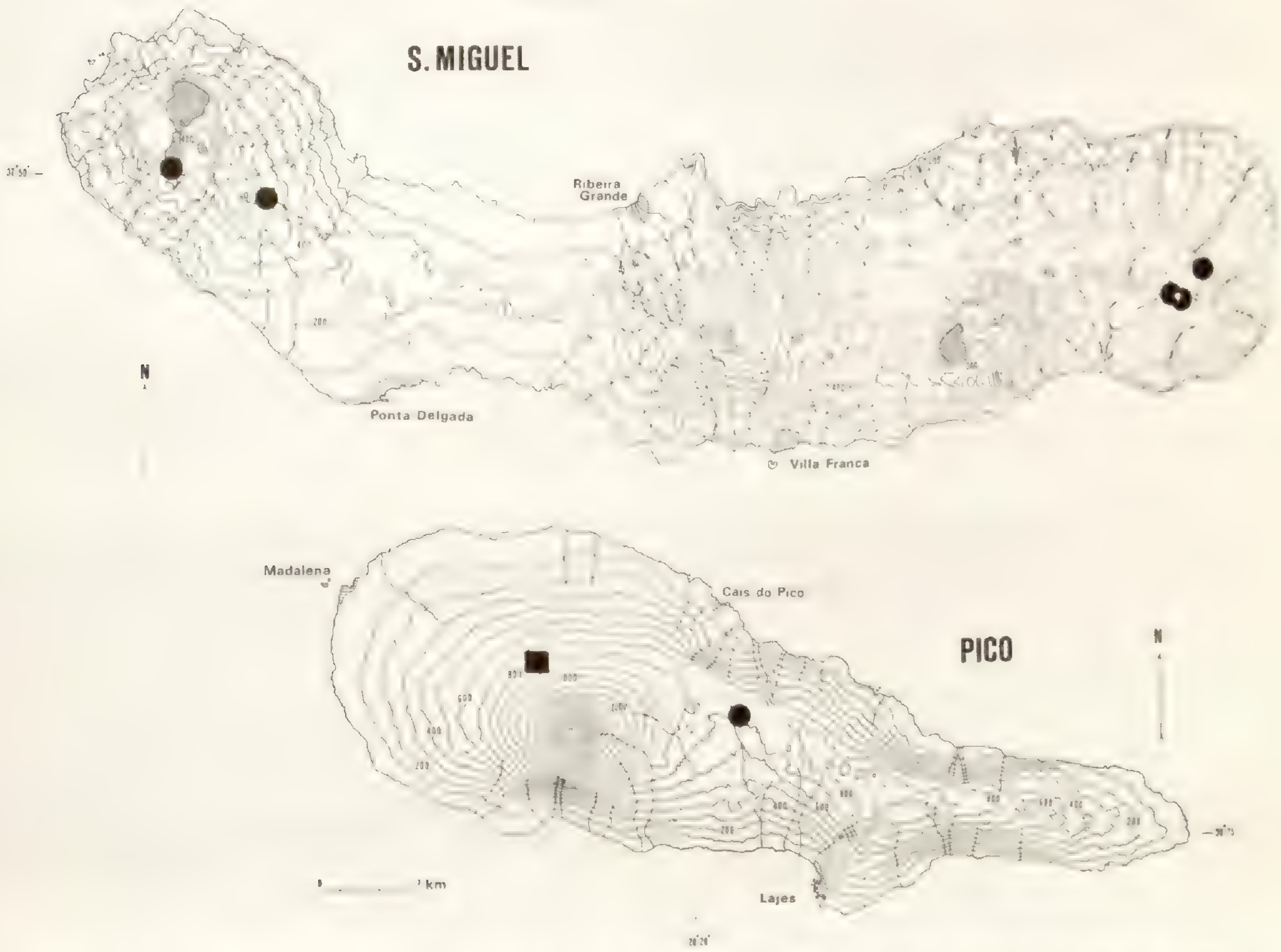

FIG. 7. ■ = *Asplenium anceps* and ● = *A. monanthes* as seen on São Miguel and Pico in 1973.

We found *A. azoricum* on all four islands visited (*Fig. 6*) and have seen specimens from all the others. This species is endemic to the Azores and is the "peculiar form" mentioned by Lovis in Palhinha (1966, p. 9). As far as we saw, it is more common on the islands than the three other members of the group. With a little experience, it is easy to recognize and differentiate from *A. trichomanes*, even at two meters distance. It prefers a higher humidity than does *A. trichomanes* subsp. *quadrivalens* and is found mainly in open, more or less north-exposed or shady situations on basalt or lava rock or walls without mortar at 200–700 m altitude. It is rarer in south-exposed places, where it stays small and

stocky. Nevertheless, sometimes it and *A. trichomanes* subsp. *quadrivalens* grow close together or intermixed. We searched such places for hybrids in vain. All plants that looked suspicious were found to produce good spores, and further examination revealed them to be specimens of one species or the other that were damaged or distorted by too dry or too shady conditions.

We thank the directors and keepers of the following herbaria for sending or letting us see valuable specimens and for photographs: B, BM, COI, K, LISU, MO, US. We specifically wish to thank Mr. J. A. Crabbe (BM) for finding the type of *A. anceps* and literature; Mr. J. B. Marshall (BM) for his help in tracing manuscripts, particularly the lists of Madeira plants by Banks and Solander, Masson and Brown, R. Brown, and others (see Britten, 1904); Mr. C. R. Fraser-Jenkins for collecting living plants of *A. heterochroum* in Bermuda; Prof. W. H. Wagner, Jr. (MICH) for living plants of both *A. heterochroum* cytotypes from Florida; Mr. G. J. de Joncheere for fronds with spores of *A. anceps* from Madeira; Prof. H. Ito and Dr. Anne Sleep for living plants of *A. tripteropus*; Prof. G. Vida for the cytological investigation of *A. monanthes* from the Azores; Prof. K. U. Kramer for the Latin diagnosis and valuable help in correcting the manuscript; and Dr. E. Sjögren for letting us use the maps of São Miguel, Pico, and Faial which he made for his monograph.

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REVIEW

"Ferns and Fern Allies of Guatemala. Part I. Ophioglossaceae through Cyatheaceae," by Robert G. Stolze, Fieldiana, Botany **39:** 1-130. 1976.—Modern floristic treatments of tropical American ferns are so few that almost any work on the subject can be said to be a welcome addition to the literature. We can rejoice that Stolze's treatment of the ferns of Guatemala and Belize far surpasses what we would accept as being a worthwhile contribution on the subject.

Some years ago, Conrad Morton agreed to do a treatment of pteridophytes for the "Flora of Guatemala", but other commitments and, eventually, ill health prevented him from proceeding much beyond the writing of preliminary keys. Be assured that the task of producing the treatment of the ferns and allies has fallen into capable hands. In this first installment, encompassing 25 genera and 110 species, Stolze treats all homosporous ferns except Polypodiaceae sensu lato. The total number of pteridophytes for the two countries will no doubt approach, or even exceed, 600 species, so that the job is roughly 20 percent completed. The format is basically the same as that used for the rest of the "Flora of Guatemala," with keys, major synonymy, descriptions, distribution, and one plate per genus. In a departure from treatments of flowering plants, plates for polytypic fern genera often include illustrations of several species. The drawings by Marion Pahl and Richard Roesener are of high quality and show important diagnostic characters well. My chief complaint (and about the only one I can muster for the work as a whole) is that I am distracted by the heavy black or densely stippled backgrounds on many plates.

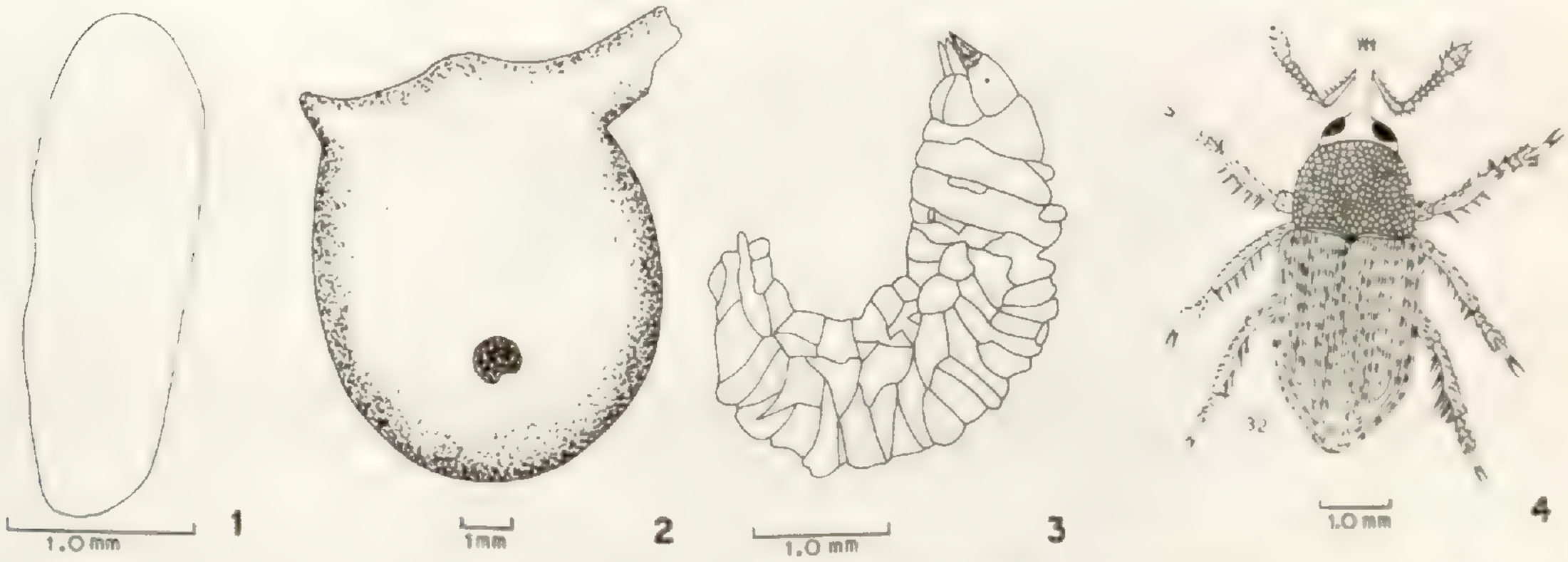
In general, Stolze recognizes modern generic and more traditional familial circumscriptions. There will no doubt be differences of opinion over circumscriptions of genera and species, but such disagreements are healthy and a natural consequence of evolution and of our inadequate knowledge of many tropical species complexes. Laudably, Stolze gives ample discussion for those taxonomic dispositions that might be subject to different interpretations and tells us where monographic work is needed to resolve taxonomic problems.

The work is nearly completely free of typographical errors. The only significant nomenclatural error that I have found is an incorrect author citation for *Gleichenia palmata* (Schaffner ex Fourn.) C. Chr. [discussed by Proctor, Brit. *Fern Gaz.* **9:** 218. 1965].

This work is a joy to use and deserves to be emulated. I eagerly await future installments.—*Alan R. Smith, University Herbarium, Department of Botany, University of California, Berkeley, CA 94720.*

SHORTER NOTES

UTILIZATION OF MARSILEA SPOROCARPS AS SHAM SEEDS BY A WEEVIL.—During our cytological sampling of natural populations of *Marsilea minuta* L. growing under terrestrial conditions in northwestern India, we found that the contents of nearly 90% of the sporocarps had been destroyed by weevil larvae of the genus *Echinocnemus* Schönherr. The larvae of the family Curculionidae, to which *Echinocnemus* belongs, often parasitize seeds, and finding them in the *Marsilea* sporocarps is a novelty. What was pointed out in 1964 by E. J. H. Corner in "The Life of Plants" (p. 181) as very similar internal structures of *Marsilea* sporocarp walls and the seed coat walls of a flowering plant, *Bixa*, has now been duly appreciated by the weevils!



Camera lucida drawings of *Echinochnemus* weevils and a *Marsilea* sporocarp. FIG. 1. Egg. FIG. 2. Sporocarp with a hole made by a larva. FIG. 3. Larva. FIG. 4. Adult.

The white, elongate eggs of *Echinocnemus* (*Fig. 1*) are laid on the soil. The larvae are internal feeders, and after hatching enter the young sporocarps by making a circular hole through the soft wall (*Fig. 2*). They are white, legless, and have prominent, brown mandibles (*Fig. 3*). The larval and pupal stages are completed in 40-45 days, and the dull brown, adult insects (*Fig. 4*) can be found close to the parasitized plants.

Weevil parasitization has an important bearing on the evolutionary biology and population structure of *M. minuta* in the Districts of Chandigarh and Amhala. The species there contains diploid and triploid cytotypes. Parasitization is undoubtedly highly detrimental to the sexual potential of the diploids, which must produce functional spores to complete their life cycle. But in the triploids, the spores are completely inviable due to meiotic upsets, and successful reproduction is exclusively by vegetative means.—*D. S. Loyal and K. Kumar, Botany Department, Panjab University, Chandigarh 160014, India.*

ECOLOGICAL AND MORPHOLOGICAL SIMILARITIES BETWEEN AN ADIANTUM AND A THALICTRUM.—The humid, rocky slopes of Tepozteco mountain in Tepozteco National Park, near the city of Cuernavaca in the State of Morelos, Mexico, support a mesophilous, mixed forest and an extensive rupicolous vegetation rich in several species of ferns. Among the ferns, adiantums are perhaps the most abundant during the rainy season. Between 1600 and 1900 m altitude we found an interesting case of ecological and morphological convergence between *Adiantum poiretii* Wikstr. (Polypodiaceae) and the herbaceous flowering plant *Thalictrum stipitatum* Rose (Ranunculaceae). Both species grow together

FIG. 1. Leaf (left) of *Adiantum poiretii* and branch (right) of *Thalictrum stipitatum*. FIG. 2. Comparison between the segments of *A. poiretii* (upper row) and the leaflets of *T. stipitatum* (lower row).

on the gentle slopes along the trails. On the natural rock walls characteristic of the area, the fern grows in crevices of the rock and *T. stipitatum* establishes itself on the soil around the base of the rocks. In both cases, the foliage of the two plants may confound the viewer, giving at first glance the impression of being the same thing. Although the branches, branching pattern, and compound leaves of *T. stipitatum* are completely different in detail from the fern leaves, the plants adopt a decumbent position and their leaflets and the fern segments have a similar outline and color (*Figs. 1* and *2*). The similarities between the plants are difficult to explain in terms of adaptive advantages for either species. It may be simply a case of coincidence, or it may be convergence caused by the habitat. Or perhaps it may be explained as an adaptation of the flowering plant which reduces predation because of the low palatability of the fern.—*Carlos Vázquez Yanes* and *Blanca Pérez-Garcia, Universidad Autónoma Metropolitana—Iztapalapa, Apartado Postal 55-532, México 13, D.F., México.*

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AMERICAN FERN JOURNAL

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Large Gametophytes of Equisetum hyemale in Northern California

MICHAEL R. MESLER and KAREN L. LU[1]

We report here the discovery of unusually large *Equisetum* gametophytes in northern California. Foster and Gifford (1974, p. 224, and references therein) state that under field conditions, mature gametophytes of *Equisetum* range from 1 mm to 1 cm in diameter and "may even be as large as 3 cm" in one tropical species

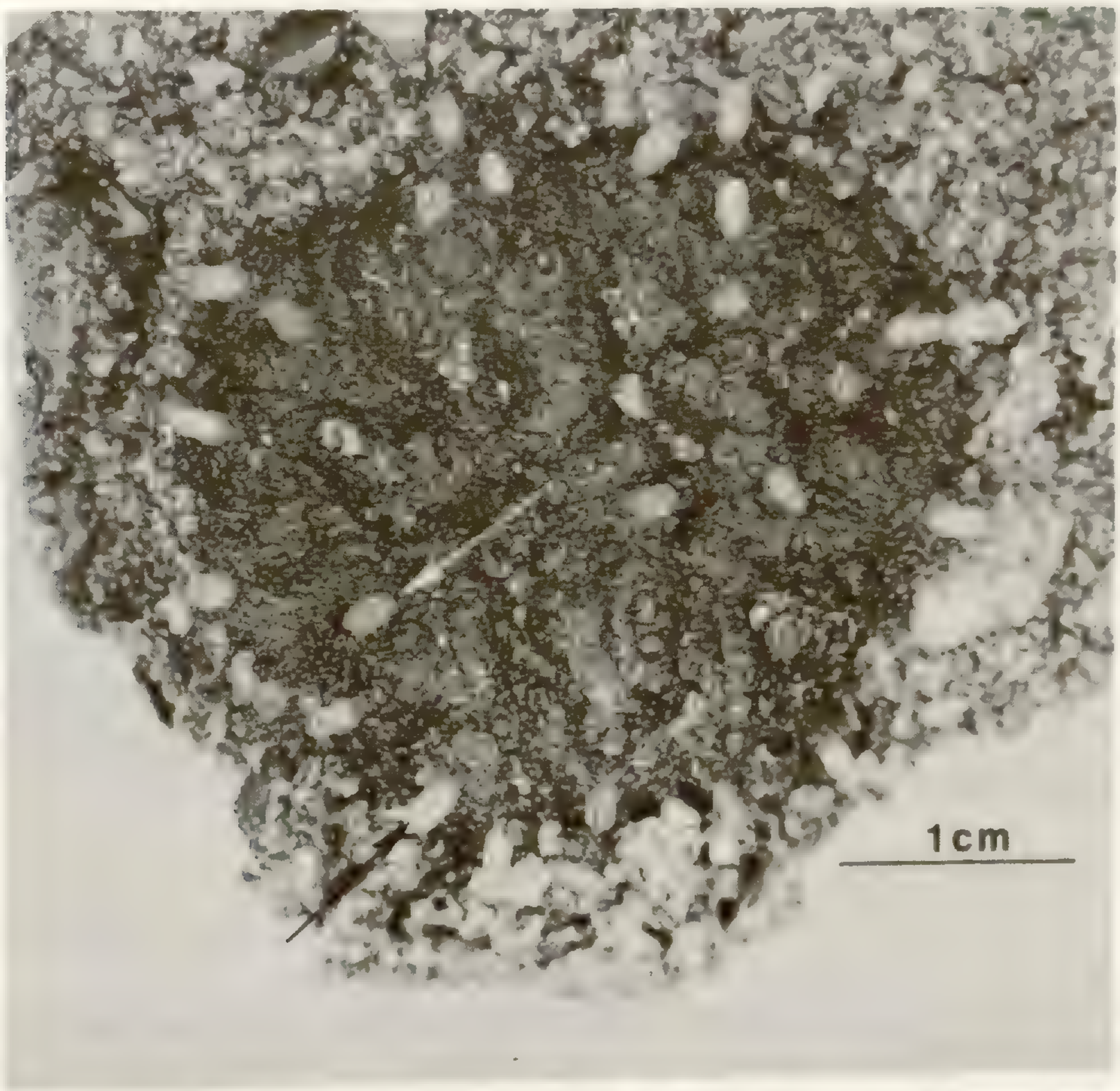

FIG. 1. Gametophyte of *Equisetum hyemale* var. *affine* with 27 emergent young sporophytes (arrows).

(see Kashyap, 1914). The largest of the gametophytes of *E. hyemale* var. *affine* (Engelm.) A.A. Eaton we found measured 3.5 cm in diameter. Of the 74 remaining gametophytes for which we have data, the mean diameter was 1.15 cm (sd= 0.42) and the range 0.4 to 2.6 cm. We regard this as a conservative description of the population, however, because approximately 150 other gametophytes that were collected at the same site two weeks earlier are not included. These were not measured, but were generally larger (hence they were the first ones we noticed and collected), and many exceeded 2 cm in diameter.

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Volume 67, number 3, of the JOURNAL was issued October 25, 1977.

The number of emergent young sporophytes produced by individual gametophytes ranged from 1 to 27 (*Fig. 1*). Although the sporophytes borne by a single gametophyte were initially crowded, we noted in specimens transplanted to the lab that horizontal shoots developed early. This behavior reduces intersporophyte competition and promotes survival of more than one sporophyte per gametophyte. Nevertheless, we were impressed by the disparity between the large number of newly emergent young sporophytes at the locality and the very small number of older sporophytes. Evidently, conditions that permit growth of gametophytes and fertilization had not existed in the recent past or, alternatively, mortality of the young sporophytes is high.

We discovered the gametophytes on moist, sandy banks of the Mad River in Humboldt County, California, near the town of Blue Lake. Collections were made in September, 1976, several months after spore release and the end of the rainy season. The range of gametophyte form and color in response to differences in exposure was similar to that reported by Kashyap (1914) and Walker (1921, 1931). We were able to identify the gametophytes by examining the anatomy of the attached young sporophytes. The sunken stomates and relatively greater development of carinal versus vallecular collenchyma indicate that the gametophytes and young sporophytes are *E. hyemale*. This is apparently the first description of the gametophytes of this species based on field collections. We emphasize the preliminary character of our findings. We do not wish to imply that the gametophytes of *E. hyemale* var. *affine* in California are always or even usually as large as the ones we discovered.

We thank D. H. Norris for alerting us to the mammoth gametophytes of the Mad River, R. Hauke for helping us to identify the material, and an anonymous benefactor who left a twenty dollar bill at the collection site.

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Anthocyanins of Azolla

Robert W. Holst*

The red-orange coloration of the aquatic fern, *Azolla*, growing in the sun is well documented (Benedict, 1923; Moore, 1969; Olsen, 1970). However, the pigments that contribute to this coloration are not known to have been identified. Harborne (1965) has identified a number of anthocyanins (3-deoxyanthocyanidins) found in the ferns *Adiantum*, *Dryopteris*, and *Pteris*. The purposes of this paper are to report on the identification of the anthocyanins in *Azolla mexicana* Presl and to describe the environmental factors which may influence this coloration.

On 15 and 28 July 1975, I collected specimens of *A. mexicana* Presl from a pond in southwestern Jackson County, Illinois. Some specimens were identified by W. Carl Taylor and me by their sporocarps, and regular and SEM photographs were made. Others of the collection were washed of epiphytes, blotted dry of excess water, and placed directly into a solution of 1% HCl in methanol. The extracted pigments were separated by one dimensional paper chromatography employing three solvent systems [BAW (n-butanol: glacial acetic acid: water, 4:1:5, top layer), 1% HCl in water, and Forestal (acetic acid: conc. HCl: water, 15:3:82)] on Whatman #1 chromatography paper (Harborne, 1967). Pigment spots were identified by visible and UV radiation and by comparing Rf values and coloration with those of published reports (Harborne, 1967). Tentatively identified anthocyanin spots were then cut out and extracted in 1% HCl in methanol and the resultant extract assayed with a Beckman DBGT Spectrophotometer to determine peak wavelength and height ratio.

TABLE 1. LUTEOLINIDIN-5-GLUCOSIDE CHARACTERISTICS OF *Azolla mexicana*.

Rf:[1]	30 (BAW), 11 (1% HC1), 35 (Forestal)
λmax:	279 nm and 495 nm (1% HC1 in MeOH)
E_{440}/E_{max} :	40% (495 nm)
Coloration:	Pink (Visible), Red (UV)

[1]One-dimensional paper chromatography separation on #1 Whatman chromatography paper employing the indicated solvents.

One visible pigment was resolved; 6 to 7 others were noted under UV radiation depending upon the solvent system employed. Of the pigments resolved, only the visible pigment displayed anthocyanin characteristics similar to those previously reported. This pigment was identified as luteolinidin-5-glucoside (*Table 1*). The other pigments as noted under UV radiation are possibly phenolic compounds; however, no attempt was made to identify them.

Luteolinidin-5-glucoside is present in all of the plant material, regardless of age. The degree of coloration is apparently due to the quantity of incident light upon

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the plant where shaded (20 klx) plants are usually green with some redness at the extreme tips of the fronds while those in direct sun (120 klx) are red-orange. Water temperature also has an effect in that plants found in a nearby, cool (15–18°C), limestone spring (pH 6.7) possess a deep purple-red coloration compared to the red-orange of plants in the warm-water (22–25°C) pond (pH 6.5).

I would like to thank Dr. John H. Yopp for his support of this research. This research was funded in part by the Illinois Soybean Program Operating Board.

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REVIEW

"FLORA OF THE LESSER ANTILLES, VOL. 2, PTERIDOPHYTA," by G. R. Proctor in R. A. Howard, published by the Arnold Arboretum, Harvard University, Jamaica Plain, MA 02130. 1977. iii + 414 pp. $25.00.—Complete and workable fern Floras for tropical American regions are published only rarely because their compilation is so laborious that few botanists have the time, resources, or inclination to undertake them. For the ferns of the Lesser Antilles, only three general works exist, the most recent of which dates from 1909, and all of which lack keys and are vastly incomplete. Thus the publication of Proctor's book, which is the first true fern Flora for the Lesser Antilles, is a major botanical event.

The Flora treats 323 species growing outside of cultivation. A conspectus down through the (conservative) family level and dichotomous keys thereafter permit ready identification of all the species. I have used the keys to a limited extent in doing identifications and have found that they worked well. Each genus is illustrated, which is helpful to non-specialists. The brief descriptions are to the point and complement the keys nicely. Geographic distribution is island-by-island for the Flora area and by country or region beyond. Habitat and abundance data also are given.

The work is of unusually high quality. In comparing it closely with my own floristic manuscript, I found only two serious errors: the placement of *Grammitis sectifrons* in *Polypodium* subg. *Phlebodium* and wrong names on *Polypodium chnoodes* (which should be *P. dissimile* L.) and on *P. dissimile* (which should be *P. sororium* Humb. & Bonpl. ex Willd.). The synonymies, so far as they go, are almost 100% correct. Errors in page numbers or publication dates are very few. The bibliography, glossary, and index are all carefully done and very helpful. In my opinion, this is the best fern Flora for a tropical American country or region yet completed, and merits a place in all pteridologists' libraries.—*D.B.L.*

The American Species of Grammitis Sect. Grammitis

L. EARL BISHOP*

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The classification of those ferns of the genus *Grammitis* with a dark, sclerenchymatous laminar border (*Grammitis* sect. *Grammitis sensu* Morton, 1967) has been considered twice in this century (Maxon, 1915; Copeland, 1952). However, during a general investigation of the grammitid ferns, it has become apparent that the delimitation of these species needs yet some clarification. It is hoped that my emphasis on a somewhat different character set will render the following treatment more faithful to the relationships in this group.

I wish to thank the staff of the U.S. National Herbarium for making this facility fully available to me. All specimens not otherwise indicated are at US.

KEY TO THE SPECIES

1. Lamina more than 3 mm wide; rhizome scales 8-12 cells wide at base.
   2. Sterile veins forked; fronds broadly rounded at the apex.
      3. Fronds with persistent, brown, pluriseptate setulae on the margin and laminar surface: lateral veins often obscure .....1. *G. marginella*
      3. Fronds with weak, hyaline, pluriseptate hairs on the margin and midrib when young, often glabrate at maturity; lateral veins clearly evident beneath.....2. *G. leptopoda*
   2. Sterile veins simple; fronds generally acuminate, acute, or cuspidate at the apex.
      4. Midrib of soriferous section of dorsal lamina generally provided with 2-3-celled simple hairs at spore maturity (may be lost in old specimens); stipes at base brown, more than 0.5 mm broad, often somewhat distant on creeping rhizome; midrib green, the sclerenchymatous sheath not exposed dorsally; laminar border 0.1-0.2 mm broad, clearly striolate under moderate magnification; hydathodes obscure or absent .....3. *G. fluminensis*
      4. Midrib of soriferous section of dorsal lamina glabrate or with branched hairs at spore maturity, or, if with 2-3-celled hairs, then stipes less than 0.5 mm broad, or the midrib blackish, the sclerenchymatous sheath prominently exposed dorsally in the basal half of the lamina.
         5. Hydathodes present; laminar border usually 0.1 mm or less wide, obscurely striolate under moderate magnification; stipe brown.....4. *G. limbata*
         5. Hydathodes absent; laminar border 0.1- 0.2 mm wide, conspicuously striolate; stipe dark brown or black .....5. *G. bryophila*
1. Lamina 1.5-3 mm wide; rhizome scales 2-6 cells wide at base.
   6. Lamina incrassate, the dark sclerenchyma of midrib not evident externally; fronds stiffly erect, congested.....6. *G. paramicola*
   6. Lamina thin, the dark sclerenchyma of midrib visible on both sides; fronds lax, spreading 7. *G. tegetiformis*

1. Grammitis marginella (Swartz) Swartz, J. Bot. (Schrader) 1800(2): 17. 1802.

Polypodium marginellum Swartz, Prod. Veg. Ind. Occ. 130. 1788. TYPE: Jamaica, *Swartz s.n.* (S not seen, photo US!).

Mecosorus marginellus (Swartz) Klotzsch, Linnaea **20:** 405. 1847.

RANGE AND HABITAT: Jamaica, Hispaniola, and Costa Rica. Epiphytic, 1500-2500 m.

This is the only species of the section with persistent, brown, setulose hairs spread over the surface of the lamina. Copeland (1952, p. 255) maintained the

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Costa Rican population to be aberrant, with respect to the insular ones, in that the fertile veinlet is not prolonged beyond the sorus and the scales are narrower. I find both characters variable in each locality and am unable to distinguish the Jamaican from the Central American plants. Actually, it is the single collection from Haiti (*Ekman H-7459*) that is exceptional; the sterile veins are simple, the laminar hairs are comparatively weak, and the texture is unusually thin for this species. But it is otherwise like the Jamaican plants and seems best referred to the same species concept at present.

2. Grammitis leptopoda (C. H. Wright in N. E. Brown) Copel. Philipp. J. Sci. 80: 255. 1952.

Polypodium leptopodon C. H. Wright in N. E. Brown, Trans. Linn. Soc. London, Bot. ser. 2, **6**: 83. 1901. TYPE: Summit of Mt. Roraima, Guyana, 8600 ft, *McConnell & Quelch 569* (K not seen, photo US!; isotype US!).

Two additional collections are at hand. *Fendler 256*, a duplicate at US of a sheet at GH, consists of two very small but identifiable plants from Tovar, Venezuela. *Bishop 812a*, from Volcán Poás, Costa Rica, differs from the type material in that the fronds are oblong, rather than being spathulate and long acuminate at the base. However, the trichomes, venation, and thin texture are characteristic of this species.

Maxon (1915), as a key character, described the rhizome scales of this species as sinuate-dentate in contrast to the entire scales of *G. marginella*. I am unable to make such a distinction. In fact, it is my observation that among the grammitid ferns in general, the size and shape of the rhizome scales are more variable than has been allowed for by most workers in the group.

The forked sterile veins, broadly rounded frond apices, and simple, pluricellular hairs seem to indicate a close relationship between these first two species. In the remaining species, the hairs are either branched or, if simple, consist of only 2–4 cells. Also, the sporangial capsules of these two species are distinctly larger (180–240 × 150–200 μm) than those of the next four (120–160 × 100–140 μm).

3. Grammitis fluminensis Fée, Crypt. Vasc. Brésil 1: 85. 1869.

TYPE: Serra do Alto Macaé, Est. Rio de Janeiro, Brazil, *Glaziou 2456* (probably P not seen; isotype S not seen, photo US!).

RANGE AND HABITAT: Jamaica, Venezuela, Colombia, and Brazil. Epiphytic, 1500–3000 m.

Two specimens at US closely match the photo of the Glaziou collection and Fée's generally good illustration: Est. Espiritu Santo, Brazil, *Mexia 4063* and Depto. Chocó, Colombia, *Lellinger & de la Sota 778*. The stomata of these plants are larger than those of the next three species, with guard cell length of 62–78 μm in this species and 46–65 μm in the others. Actually, since in a given specimen stomatal length tends to vary inversely with the width, an index of length times width renders a more accurate description of stomatal size. Such an index of stomata measured of *G. fluminensis* gives 3000–4030; pooled values of the next three species yield 1970–2900.

Three collections from Jamaica exhibit smaller fronds, but the trichomes, the wide brown stipes, the generally obscured midrib, and large stomata place them

with *G. fluminensis*. However, several sheets from Venezuela are more problematic. These agree with the other plants referred here in their wide stipes and large stomata, but differ in their narrowly attenuate laminar bases, and, more critically, in their small but distinct hydathodes. Presence of hydathodes is generally a taxonomically important character among the grammitid ferns, but since the material is limited, I choose not to segregate this population nomenclaturally from others to which it seems clearly related.

The difficulty in separating *G. fluminensis* from the next two species in the key by macroscopic characters stems from the occasional occurrence of large individuals in both *G. limbata* and *G. bryophila*. Such plants of the former are glabrate at maturity or bear branched trichomes. Also, the foliar border is generally less than 0.1 mm broad and obscurely striolate. In the latter species, larger specimens seem always to have the perivascular sclerenchyma of the midrib prominently exposed dorsally in the lower half of the frond.

4. Grammitis limbata Fée, Gen. Fil. 233. 1852; Mém. Foug. 6: 6, t. 5, f. 1. 1854.

Grammitis nigro-limbata Spruce ex Hooker, Sp. Fil. **4:** 164. 1862, *nom. nud. in synon.*

Polypodium nigro-limbatum Jenm. Bull. Bot. Dept. Jamaica, ser. 2, **4:** 69. 1897, *nom. superfl.*

Polypodium marginellum var. *brasiliense* Rosenst. Hedwigia **46:** 135. 1906. TYPE: Serra Ikerim, Est. Santa Catarina, Brazil, *Schmalz 163* (S not seen; isotype UC!).

Polypodium limbatum (Fée) Maxon, Bull. Torrey Bot. Club **42:** 222. 1915.

Polypodium hessii Maxon, Bull. Torrey Bot. Club **42:** 223. 1915. TYPE: Sierra de Naguabo, Puerto Rico, *Hess 312* (US!)

Grammitis nigrolimbata (Jenm.) Lellinger, Proc. Biol. Soc. Washington **89:** 715. 1977, *nom. superfl.*

TYPE: Guadeloupe, *Perrottet s.n.* in 1824 (presumably P or RB not seen).

RANGE AND HABITAT: Jamaica, Hispaniola, Puerto Rico, Guadeloupe, St. Vincent, Brazil, and Bolivia. Epiphytic, generally at lower elevations than other species of the group, 600–1600 m.

Although I have not seen the type, only one species of the section is known from Guadeloupe, so that the name may be applied with reasonable certainty. I include here those plants with distinct hydathodes and narrow laminar borders. The Caribbean populations generally have much branched trichomes on the margin and on the lamina near the midrib. In the Bolivian specimens, such hairs are reduced and often simple; in this respect they are rather similar to *G. fluminensis* and *G. bryophila*. However, in these plants the marginal hairs tend to be persistent, as is true of the species as a whole, whereas in the other two species the marginal trichomes are promptly deciduous.

The nomenclature of this species concept relative to the next is somewhat complicated, particularly with respect to the name *Polypodium nigrolimbatum*. The epithet first appeared associated with *Grammitis* as a synonym for Hooker's concept of *P. marginellum* Swartz. Its source is attributed to a manuscript of Spruce. In Jenman's publication of the name under *Polypodium*, he cites as synonyms not only Spruce's name but also "*Grammitis nimbata* Fée." It therefore seems clear that he wished to provide a new epithet for his concept due to the prior existence of *P. nimbatum* Jenman. Unfortunately, there is no *G. nimbata* Fée. I propose that Jenman really had *G. limbata* Fée in mind and that the letter

change mistakenly became incorporated into his manuscript, causing him to think the new name necessary. Following this interpretation, *P. nigrolimbatum* Jenman becomes a superfluous nomenclatural synonym of *G. limbata* Fée. Jenman's concept was evidently broader than mine, for he cites a "wide range" for the species in South America. But, Copeland's (1952, p. 260) implication to the contrary, he does not mention *G. fluminensis* in connection with this species.

Maxon (1915) restricted his concept of *P. limbatum* to the Lesser Antillean populations. The plants from Porto Rico he segregated as *P. hessii*, differing "in its more rigid and darker rhizome scales, in its nearly basal sori, and in its distinctly stipitate (rather than nearly or quite exstipitate), narrower, attenuate fronds." Like Copeland, I find these characters weak. Of the two sheets I have seen from Guadeloupe, one shows stipitate fronds and elsewhere this character is variable. As for the soral position, the discrimination of small differences seems of little value in these and other grammitid ferns. The paleae are paler in the Guadeloupe plants than is usual elsewhere, but again this is scarcely an invariable character trait. Far more significantly, the Guadeloupe specimens are unique in their broad (0.1–0.2 mm), thin, flat laminar borders. Certainly distinctive, should further material prove this reasonably constant, a subspecific designation might be in order. However, since these plants agree with others in their prominent hydathodes and branched hairs which are subpersistent on the margin, and since I have seen few specimens, I prefer not to segregate them nomenclaturally. Interestingly, the St. Vincent material is more like that of Puerto Rico and Jamaica than of Guadeloupe.

Maxon included under *P. nigrolimbatum* Jenman all the similar plants of Jamaica and South America (the Costa Rican population was unknown at the time). By doing so, he clearly showed his interpretation of Jenman's publication to differ from mine; i.e., he considered Jenman to have presented his name to apply to a new, previously unrecognized concept. Maxon lists *G. fluminensis* Fée as a synonym (the epithet has a prior application in *Polypodium*).

Copeland's treatment of this and related species was similar. He does suggest that *P. hessii* is probably not distinct from the Lesser Antillean plant, but his concept of *G. fluminensis* is essentially like that of Maxon's *P. nigrolimbatum*, and among the specimens he cites are plants of both Jamaica and Bolivia which I recognize as *G. limbata*, as well as others which I refer to the following species.

Through the kindness of Dr. Alan R. Smith I have been able to examine the isotype of Rosenstock's hitherto obscure *Polypodium marginellum* var. *brasiliense*. Although the plant is rather small, it is nonetheless quite similar to the Bolivian specimens mentioned above that I refer to this species.

5. Grammitis bryophila (Maxon) Seymour, Phytologia 31: 172. 1975.

Polypodium bryophilum Maxon, Amer. Fern J. **16:** 7. 1926. TYPE: Vicinity of La Palma, on the road to La Hondura, Pcia. S. José, Costa Rica, *Maxon & Harvey 7980* (US!).

Polypodium haplophlebicum A. C. Smith, Bull. Torrey Bot. Club **58:** 307. 1931. TYPE: Mt. Duida, Edo. Bolivar, Venezuela, *Tate 553* (NY!; isotype US!)

Grammitis haplophlebica (A. C. Smith) Vareschi, Fl. Venez. **1:** 872. 1969.

RANGE AND HABITAT: Costa Rica, Venezuela, Colombia, and Bolivia. Epiphytic, 1500–3000 m.

Maxon's type stands apart from all other specimens included here in its much broader fronds (up to 8 mm) and the correspondingly greater divergence of the veins from the midrib (40–50°). The resulting aspect of the plant is so distinctive that the wish to segregate it specifically is certainly understandable. However, I detect no other unique characters. Until further collections are made to clarify its status, I prefer to regard it as a large variant of a species normally with fronds 3–5 mm wide and with veins diverging at an angle of 30–40°.

The type of *P. haplophlebicum* is more typical; although smaller than is average for the species, it is no more so than specimens from elsewhere.

This species is separable from *G. fluminensis* by its smaller stomata, dark brown or black stipes, and by the perivascular sclerenchyma of the midrib, which is usually exposed prominently in the basal half of the frond on the abaxial side. From *G. limbata* of generally lower altitudes it differs most conspicuously in its lack of hydathodes, as well as in the other characters cited in the key.

6. Grammitis paramicola L. E. Bishop, sp. nov.

Filix terrestris altitudinis celsae andinae. Rhizoma ascendens, frondes dense confertas ferens paleisque onustum 2–3 mm longis apicibus filiformibus ad basin 4–6 cellulis latis. Stipes brevis 1–5 mm basin versus teres 0.2–0.4 mm diametro. Lamina 2–7 cm × 1.5–3 mm, incrassata stricta linearis base acuminata, ad apicem rotundata vel acuta aliquando cuspidata, venationem et costae vaginam atrofuscam perfecte obruens, margine sclerotico striolato 0.15–0.20 mm lato, ubi juvenis pilis brevibus subclavatis ex 2–3 cellulis constantibus in pagina praedita autem semper margine glabra, stomatibus abaxialibus 45–55 × 36–45 μm, sorifera per partem quartam vel dimidiam distalem 1–2 mm apicis exceptis. Venae steriles simplices liberae, illae fertiles furcatae, furca acroscopica brevi prorsum receptaculari, basiscopica libera aut cum vena distali proxima prope marginem conjungenti. Sori sub maturitate confluentes et haud distincti, receptaculis parum inframedialibus saepe ad costam paene parallelis nonnunquam linealiter contingentibus. Sporangia capsulis 140–155 × 120–140 μm sporisque globosis 22–26 μm diametro.

HOLOTYPE: Near the Huila–Caquetá divide, 25 km SE of Gigante, Depto. Huila, Colombia, uncommon on bare areas of soil with lichens in paramillo, 11,000 ft. *E. L. Little, Jr. 8663* (US).

PARATYPES: Huadquiña, Depto. Cuzco, Peru, 9000 ft, *Buës 1271* (US); Playapampa, Depto. Huánuco, Peru, *MacBride 4520 (US)*.

Although abundant in adjacent cloud forests, few grammitid ferns characteristically inhabit the tropical American páramo. The narrow, stiffly erect fronds and the thick lamina which completely hides the lateral venation in this species are perhaps adaptations to this environment, as other paramicolous ferns show similar growth forms.

7. Grammitis tegetiformis L. E. Bishop, sp. nov.

Grammitis tenera in saxis rivorum tegetes formans. Rhizoma parvulum repens paleis minimis 1 mm longis aut minus ad basin truncatis vel cordatis, 2–5 cellulis latis. Stipites 1–2 mm, non conferti, ad basin teretem 0.15–0.2 mm

diametro. Lamina 1–3 cm × 1.5–2 mm, tenuis chartacea lineari-spathulata, basin versus sensim acuminata, ad apicem rotundata, costae vagina atrofusca in dimidio inferiore utrinque manifesta, margine sclerotica angustissima 0.04–0.06 mm lata interdum vix evidenti, ubi juvenis pilos hyalinos simplices vel multifurcatos in aut prope costam gerens etsi postea glabra, stomatibus abaxialibus 43–53 × 36–41 μm, sorifera per partem distalem. Venae vix visibiles liberae hydathodis carentes, eae steriles simplices, eae fertiles aut simplices aut furcatae furca acroscopica brevi receptaculari. Sori inframediales pauciores impressi ex pagina ventrali gibborum similes protrudentes. Sporangia capsulis 180–200 × 140–160 μm, cellulis annularibus 9–11, sporisque globosis 24–29 μm diametro.

HOLOTYPE: Vicinity of "Drizzly Camp," summit of central western part of Auyan-tepuí, along dry stream bed of branch of Río Churúm, Edo. Bolívar, Venezuela, on sandstone boulders, 1760 m, *Steyermark 93343* (US).

This is quite the smallest of all known species of sect. *Grammitis*. It differs from other American species in the evidence of the dark costal sheath on both sides of the frond, and also in the very narrow laminar border which is invisible to the unaided eye and difficult even to detect with a hand-lens. The exact relationship of this species is unclear. The very thin texture is reminiscent of both *G. leptopoda* and *G. limbata*. With the former it agrees significantly in the larger sporangial capsules, but differs in the usually branched trichomes and simple sterile veins. The branched hairs suggest *G. limbata*, but the lack of hydathodes and the sporangial size would seem to remove the possibility of a close affinity. The type collection is notable for the presence of gametophytes and young sporophytes in all stages of development.

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Cheilanthes kuhnii var. brandtii and the Composition of its Farina

SHUNSUKE SERIZAWA* and ECKHARD WOLLENWEBER**

Cheilanthes kuhnii Milde var. *brandtii* (Fr. & Sav.) Tagawa is a fern endemic to central Honshu in Japan. This fern is morphologically characterized as follows. The fragile stipes are 8–20 cm long, castaneous, and bear broadly lanceolate, pale brown scales on the lower parts. The laminae are narrowly ovate, tripinnatifid, 15–30 cm long, and 6–13 cm wide. They are summer-green, thinly herbaceous, and more or less farinose beneath. The indusia are continuous in fully soriferous leaves, but sometimes are interrupted in less soriferous ones.

According to Ching (1941), this fern belongs to *Aleuritopteris* sect. *Dalhousiae*, characterized by not or thinly farinose laminae and relatively thin texture. He regarded it as being identical with *C. kuhnii* Milde var. *kuhnii* of Korea, Amur, Manchuria, and North China. But typical *C. kuhnii* of the mainland of Asia has lanceolate and rather deeply dissected laminae. The Japanese plants seem to be more appropriately treated as a variety of *C. kuhnii*.

Cheilanthes kuhnii var. *brandtii* is usually not rare in the habitats where it grows, but its geographical range is limited to the limestone areas of central Honshu. It is usually found in rather open, dry, and more or less disturbed places, such as on roadside rocks or stone walls near villages, but rarely is found on moist and shaded rocks deep in the mountains. The density of the white farina on the lower surface of the lamina is strongly influenced by the habitat. The plants in open and dry places bear a considerable amount of farina, whereas those in moist and shaded places are hardly farinose. Makino (1917) described var. *efarinosa* having non-farinose laminae, but it seems to be only an extreme form not worthy of varietal distinction.

As part of a screening program on flavonoid excretion in farinose species of the Gymnogrammoideae, the farina of *C. kuhnii* var. *brandtii* has been analyzed. Akahori (1976) reported on the occurrence of glycosides of kaempferol and quercetin in the leaf tissue of this fern, but no chemical investigation of its farina composition has been published hitherto.

Twelve grams of air-dried fronds, collected in September 1976 (Pref. Gunma: Tsuchiya-sawa, Shimonita-machi, *Serizawa 25920*, TNS) were rinsed with acetone to dissolve the external mealy deposit. The yield was about 450 mg. This material consists of a small amount of (unknown) lipoids and of flavonoid aglycones. By preparative chromatography on a column packed with polyamide, the latter components could be separated. They were identified by thin layer chromatographic comparison with authentic substances and by measurement of their UV spectra (cf. Wollenweber, 1975a). Thus, the following compounds could

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be detected: Kaempferol, 3,7,4′-trimethyl ether and kaempferol 7,4′-dimethyl ether are the major components. Apigenin 4′-monomethyl ether (acacetin), and apigenin itself are minor components. Besides these, there are trace amounts of kaempferol 3,7-dimethyl ether (kumatakenin), kaempferol 3,4′-dimethyl ether (ermanin), kaempferol 3-methyl ether (isokaempferid), and perhaps apigenin 7-methyl ether (genkwanin).

Flavones and flavonols usually occur in plant tissue as glycosides, i.e. as water-soluble compounds in the cell sap. Rather rarely they occur as aglycones in plants excreting lipophilic materials, as, for instance in buds of some trees like poplars (Wollenweber, 1975b). Flavonoid exudates also are known to form an external mealy deposit on *Primula* species (Wollenweber, 1974) and on ferns of the genera *Cheilanthes, Notholaena,* and *Pityrogramma*. In the latter genus, chalcones and dihydrochalcones are abundant, being responsible for the white and yellow coloration on silver-back and gold-back ferns (Wollenweber, 1976a). In *Cheilanthes* and *Notholaena*, the farina mostly consists of methylated flavones and flavonols (Wollenweber, 1976b, 1977). This ís also true for *Cheilanthes kuhnii* var. *brandtii*, as was shown above. The pattern expressed here resembles especially that of some of the almost 50 representatives of *C. farinosa* (Forsk.) Kaulf. so far examined, but is not precisely identical with any of them. Unfortunately, it was not possible to compare the pattern with a sample of *C. kuhnii* var. *kuhnii*. It is of interest that kaempferol is found to occur in glycosidic form in the leaf tissue, as well as in the form of methyl ethers deposited externally. Quercetin, on the other hand, is present only in the tissue, whereas the farina in addition contains methyl ethers of the flavone apigenin.

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———. 1977. Die Zusammensetzung des Flavonoid-Mehls bei einigen Farnen. Zeitschr. Pflanzenphysiol. **85:** 71–76.

The Correlation of Morphology and Geographical Distribution in Lycopodium saururus

CRISTINA ROLLERI*

The leaves of *Lycopodium saururus* Lam. exhibit several features that vary in relation to certain environmental factors. The wide geographical distribution of this species led de la Sota (1972) to suggest that possibly a complex was involved. The present analysis is part of an attempt to solve the systematic problems of *L. saururus* and to elucidate its relationships with allied species, with which it shares the following characters. The plants are terrestrial or saxicolous and grow in tropical or subtropical regions, especially at medium to high elevations in mountains; their stems are columnar, finger-like, erect or ascending, and can be succulent or herbaceous, but generally are stiff or sometimes very rigid, with radial symmetry and dichotomous branching; their microphylls are isomorphic; distinct fertile areas or well-defined strobili are never produced.

Lycopodium saururus is included in series *Eusaurura* Herter of section *Crassistachys* Herter (Herter, 1949, p. 72). In Herter's sense, series *Eusaurura* does not include all the species I believe are allied to *L. saururus*. Section *Crassistachys*, even if it may prove to be natural, was based on insufficient morphological analysis. Nomenclatural details concerning *L. saururus* will be presented in a forthcoming paper.

MATERIAL STUDIED

CENTRAL AMERICA: Costa Rica: PCIA. CARTAGO: Among rocks in the páramo of Cerro de la Muerte, Cordillera de Talamanca, *Williams 20025* (US); Paramillo on Cerro de La Muerte, Cordillera de Talamanca, along Panamerican Highway, *Williams et al. 28833* (US); Páramo de Cerro de La Muerte, Cordillera de Talamanca, *Williams 16087* (US); Cerro de La Muerte, Panamerican Highway, *Carpenter 299* (US). PCIA. S. JOSÉ: Cerro de Las Vueltas, *Standley & Valerio 44004, 44006, 43611* (all US); Cerro de La Muerte, La Virgen de Los Angeles páramo, *Brown 88* (US); 0.55 km towards Cartago from San Isidro del General, *McKee 11203* (US); Páramo Buena Vista, 1-3 km S of the Interamerican Highway, *Lellinger 869, 870* (both US); Páramo Buena Vista, 1-3 km S of the Interamerican Highway, *Mickel 2117, 2118* (both US); Páramo Buena Vista, *de la Sota 5047* (LP, US); Pseudopáramo on Buena Vista Massive, 33 mi NW of San Isidro del General, 5 km NW of La Georgina, *Woodruff* (US 2551951). **PANAMA:** PCIA. CHIRIQUÍ: Loma Larga to summit, Volcán de Chiriquí, *Woodson & Siebert 1079* (US).

SOUTH AMERICA: Venezuela: EDO. TACHIRA: Páramo de El Colorado, continuación de El Zumbador, cumbre del páramo, *Cuatrecasas et al. 28282, 28283* (both US). EDO MERIDA: Laguna Coromoto-Laguna Verde, *Aristeguieta 2625a* (VEN). **Peru:** DEPTO. CUZCO: Acanacu, *Vargas 355* (GH). DEPTO. JUNÍN: Pcia. Huancayo, Laguna Huacracocha, *Soukup 3744* (US); Nevado Sallcantay, *Buës 744* (US); Cerro Huaytapallana, *Tryon & Tryon 5469* (US); San José, *Macbride & Featherstone 1111* (US). DEPTO. LA LIBERTAD: Pcia. Santiago de Chuco, Jalca de Quesquenda, *Sagastegui 4542* (GH); Jalca de Quiruvilca, *Sagastegui 2874* (GH). **Bolivia:** DEPTO. COCHABAMBA: Chapare, *Steinbach 9750* (GH); San Benito (Chapare), *Steinbach 9799* (NY); Choro, Aparcita, above the Cocapata River, ca. 100 mi from Cochabamba, across the Tunari Range, *Brooks 6095* (NY); Cordillera Real, Alaska Mine, *Tate 52* (NY); La Fabulosa, tin mine at the head of Challana valley, *Brooks 6347* (NY). DEPTO. LA PAZ: Yungas, Unduavi, *Rusby 453a* (NY). **Argen-**

---

*Museo de La Plata, La Plata, Bs. As., Argentina

tina: PCIA. JUJUY: Volcán, Loma del Tambo, *Schreiter 2559, 4111* (both LIL); Volcán, Mula Muerta, *Castillon 218* (LIL); Tumbaya, Filo del Vallecito, Cerro Horqueta, *Cabrera et al. 16978* (LP); Tumbaya, Abra del Cerro Morado, *Fabris et al. 6325* (LP, US); Tilcara, Falda Grande, Cerro Huaira-Huasi, *Cabrera & Hernandez 14003* (LP); Valle Grande, Cerro Hermoso, *Fabris et al. 5827, 5921* (both LP); Santa Barbara, Cerro El Centinela, *de la Sota 2884* (LP); Capital, Abra Delgada, entre León y Nevado de Chani, *Fabris et al. 4188* (LP). PCIA. SALTA: Oran, Cerro Questo Asentado, *Peirotti 1036* (LIL); Santa Victoria, camino a Santa Victoria, *de la Sota 4118* (LP, US); Santa Victoria, entre Lizoite y Rodeo Pampa, *Meyer* (LIL, US 1564924); Pampa Grande, *Spegazzini* (SI 21251); Candelaria, Cerro Chorrillos, *Venturi 3844* (SI); Caldera, subida al Nevado del Castillo por El Mal Paso, *Sleumer & Vervoorst 2910* (LIL, US). PCIA. CATAMARCA: Ambato, El Creston,

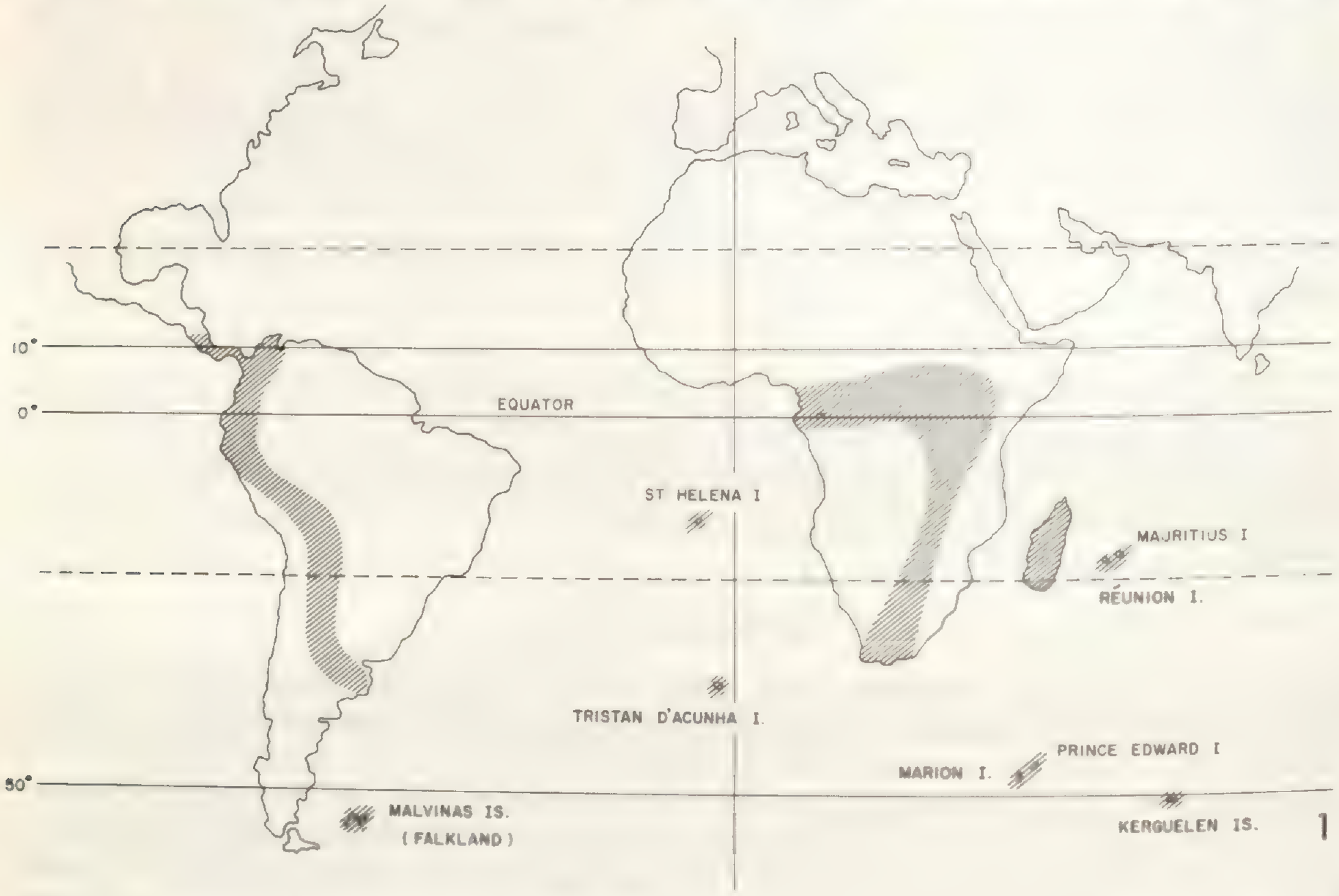

FIG. 1. Geographical distribution of *Lycopodium saururus*.

Castillon 11542 (LIL), *92290* (US 2084230); Andagalá, *Jörgensen 106* (SI); Capallan, Los Angeles, *Peyrano* (GH). PCIA. TUCUMÁN: Tafi, La Quenoa, *Parodi 18773* (GH); Tafi, Río Blanco, *Castillon* (LIL 92362); Tafi, Cumbre NE de La Ciénaga, *Schreiter 1031* (LIL); Tafi, Cumbre de Mala Mala, *Lillo 2720* (LIL); Tafi, Tafi del Valle, *Sparre 5724* (LIL); Tafi, Valle de San José, La Banderita, *Sparre 5904* (LIL); Tafi, La Hoyada, *Venturi 2848* (SI), *Castellanos 14616* (LIL); Tafi, Quebrada Honda, *Sparre 9274* (LIL); Tafi, Carapunco, Infiernillo, *Lamb 5389* (LIL); Río Chico, Escaba, *Monetti 1906* (LIL); Trancas, Las Burras, *Chavez* (LIL 442298); Chicligasta, La Pavas, *Castillon? 3038* (GH, SI, US). PCIA. CÓRDOBA: Sierras de Córdoba, *Lorentz 1783* (US); Sierra de Achala, *Hieronymus* (US 1431706), *Hieronymus* (US 594600); Pampa de Achala, *Hunziker 1426* (US), *6477* (LP, US), *Rentzell* (SI, US).

ISLAS MALVINAS (FALKLAND ISLANDS): *1839 - 43 Antarctic Expedition* (GH).

AFRICA: Ethiopia: East slopes of Mt. Delo, Amaro Mountains, southern Ethiopia, *Gillet 15048* (US). **Democratic Republic of the Congo:** Volcan Karisimbi, au NE du Lac Kivu, *Humbert 8567* (US; Mt. Kahuvi, W. of Lake Kivu, *Cambridge 1959 Congo Exped. 465* (US). **Kenya:** Aberdare Range, Mt. Aberdare, sul Kinangop, *Balbo 405* (US); Maïbey Swamp, Cherangani Hills, *Tweedie 3400* (US) West slopes of Mt. Kenia, along the trail from West Kenia Forest Station to summit, *Mearns 1463, 1498, 1457* (all US).

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MADAGASCAR: Iratsy, Massif de l'Andringitra, vallées de La Riambava et de l'Antsifotra, *Humbert 3925a, 3925b* (both US).
RÉUNION: "Pelousse altimontaine du Plateau Kerveguen," 2200 m alt, *Badré 936* (US).
KERGUELEN ISLAND: *Eaton* (GH).
PRINCE EDWARD ISLANDS: Marion Island, Challenger Exped., *Moseley* (GH).

GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Lycopodium saururus is confined almost exclusively to the southern hemisphere (*Fig. 1*). Its distribution is as follows.

In the New World, its grows from 10°N to 35°S Lat. in Costa Rica, Panama, and in the western Andean region of South America from Venezuela to northwestern Argentina, where it spreads eastward to the Sierras Subandinas and the Sierras Pampeanas of northwestern and central Argentina and the Sierras Australes (Ventania system) of Buenos Aires province. The connections between these ranges seem to be more or less clearly established (Frenguelli, 1950) and afford adequate geographic and ecologic continuity to the dispersal of this typically montane species.

TABLE 1. ALTITUDINAL RANGE OF *Lycopodium saururus* THROUGHOUT ITS GEOGRAPHICAL RANGE.

Region	*Altitudinal range* (m)
Central America	2500–3500
South America	
Andes	3000–5000
Sierras Subandinas	2000–4000
Sierras Pampeanas	1500–2500
Sierras Australes	1000–1200
Africa	2500–5000
Madagascar	2000–3500
Réunion	2200

In Africa it grows from 8°N to 36°S Lat. on the high mountains of the tropical and subtropical region, from southern Ethiopia (Aberdare Range) through Kenya, the Congo, Uganda, Zambia, Tanzania, and Rhodesia to South Africa (Cape Town, Natal).

Among the islands of the south Atlantic Ocean, it is known from 15°S to 37°S Lat. on St. Helena and Tristan d'Acunha. It occurs from 15°S to 50°S Lat. on the Indian Ocean islands of Réunion, Mauritius, Madagascar, Kerguelen, and Marion.

Lycopodium saururus inhabits exclusively medium- to high-elevation mountains, and has a wider range of elevation in continental areas than on islands (*Table 1*). The elevation range in America is wider than in Africa, although it is uncommon below 2000 m on both continents. The ecological continuity provided by the peripampasic arch (Frenguelli, 1950) or "arco serrano" (de la Sota, 1967) favors its appearance at greater latitudes and lower heights, down to the Sierra de la Ventana in Buenos Aires province.

ECOLOGY

Lycopodium saururus grows on permanently or densely clouded slopes or on those with a considerable seasonal rainfall. Occasionally it is found in more exposed areas with less humidity and higher radiation, but in this case the colonies are smaller, with lower density, and contain smaller plants.

Soil seems to be an important factor. *Lycopodium saururus* lives on acid, peaty soils rich in organic materials and which have abundant soil moisture, including swampy or periodically inundated places. Low temperatures do not seem to be a limiting factor, and plants can be found at high altitudes, although below the permanent snow line.

In Costa Rica and Panama *L. saururus* grows on high mountains and volcanos, on humid slopes protected by other plants or stones. In Costa Rica it grows on the "páramos without *Espeletia*" (Cuatrecasas, 1968), or pseudopáramos, marshes, or high swamps, associated with *Sphagnum*, or on open, grassy areas with species of *Chusquea, Senecio, Hypericum*, etc.

In Venezuela, Colombia, and Peru it grows in subpáramo, in the páramo proper,[1] and in superpáramo (Cuatrecasas, 1968), associated with the flora characteristic of each. It is more abundant in the páramo proper, where climatic, edaphic, and thermic conditions seem to be most favorable for its development.

In Peru, Bolivia, and Argentina it grows in humid puna and high mountain communities, generally on the eastern slopes of the Andes. On cloud-covered mountains in Peru and Bolivia it is associated with a rich flora of hepatics, pteridophytes, and angiosperms.

In northwestern Argentina it occurs in moorlands ("vegas de altura"), grassy swamp areas, or protected by stones near streambanks. In the Sierras Pampeanas and Australes, it occurs in similar situations, in grasslands, low woods, and in general near streams protected by other plants or rocks.

MORPHOLOGY AND DISTRIBUTION

Previous studies on the group (Rolleri, 1970, 1972, 1974, 1975, in press; de la Sota & Rolleri, 1972) have led to two main lines of analysis: the study of leaf morphology, especially the epidermis, stomata, and epidermic modifications, and the study of sporangium morphology, especially its epidermis. The former has been very useful in solving systematic problems because of specific and intraspecific variation of a certain number of characters useful in separating the species, subspecies, and varieties. Although studies of the latter kind are rare and mostly quite recent (Englert, 1925; Rolleri, 1972, 1974, 1975, in press; Øllgaard, 1975), these investigations are important because characters of the sporangium vary at the specific and infraspecific levels. It is also possible to determine the degree of maturity of the plant by knowing the stage of development of the

---

[1] In northern Peru, the term "jalca" is equivalent to what is termed páramo in central and southern Ecuador. Because the former is a vernacular term, I have adopted the latter, which has been scientifically defined.

sporangium wall (Rolleri, in press), which allows one to determine plants with incipient fertility or to recognize juvenile forms that resemble adult specimens (and so avoid these in taking measurements). The different stages of sporangium wall development can be correlated with definite stages of sporogenesis.

Both kinds of morphological studies are the basis for the present comparative study, which was carried out on *L. saururus* specimens from different parts of its distribution. Measurements were taken from 25 leaves from the median portion of each adult stem. Basal and terminal leaves were avoided to eliminate taking measurements from aged, modified, or juvenile leaves. Twenty-five stomata were measured on each of 25 leaves (625 stomata per branch) for diameters and density. The total of measured plants was 58 for America, ten for Africa and Madagascar, and one each for Réunion, Kerguelen, and the Prince Edward Islands. But on specimens borrowed from the Gray Herbarium (three for Venezuela and one each for Bolivia, the Malvinas, Kerguelen, and Prince Edward Islands), only the dimensions of the leaves were measured due to the impossibility of processing leaves for clearing.

The leaves of *L. saururus* are lanceolate and isomorphic (the sterile and fertile are alike), with straight to inflexed, acute apices. They are thick or nearly so, slightly succulent, and have a smooth, glossy surface and papillose margins. The leaves are smooth and convex on both faces, not keeled, erect and stiff but not rigid. They become papyraceous and break easily, when dry, and so differ from those of other allied species (e.g., *L. crassum* Humb. & Bonpl. ex Willd.), which are always coriaceous and very rigid, even when dry.

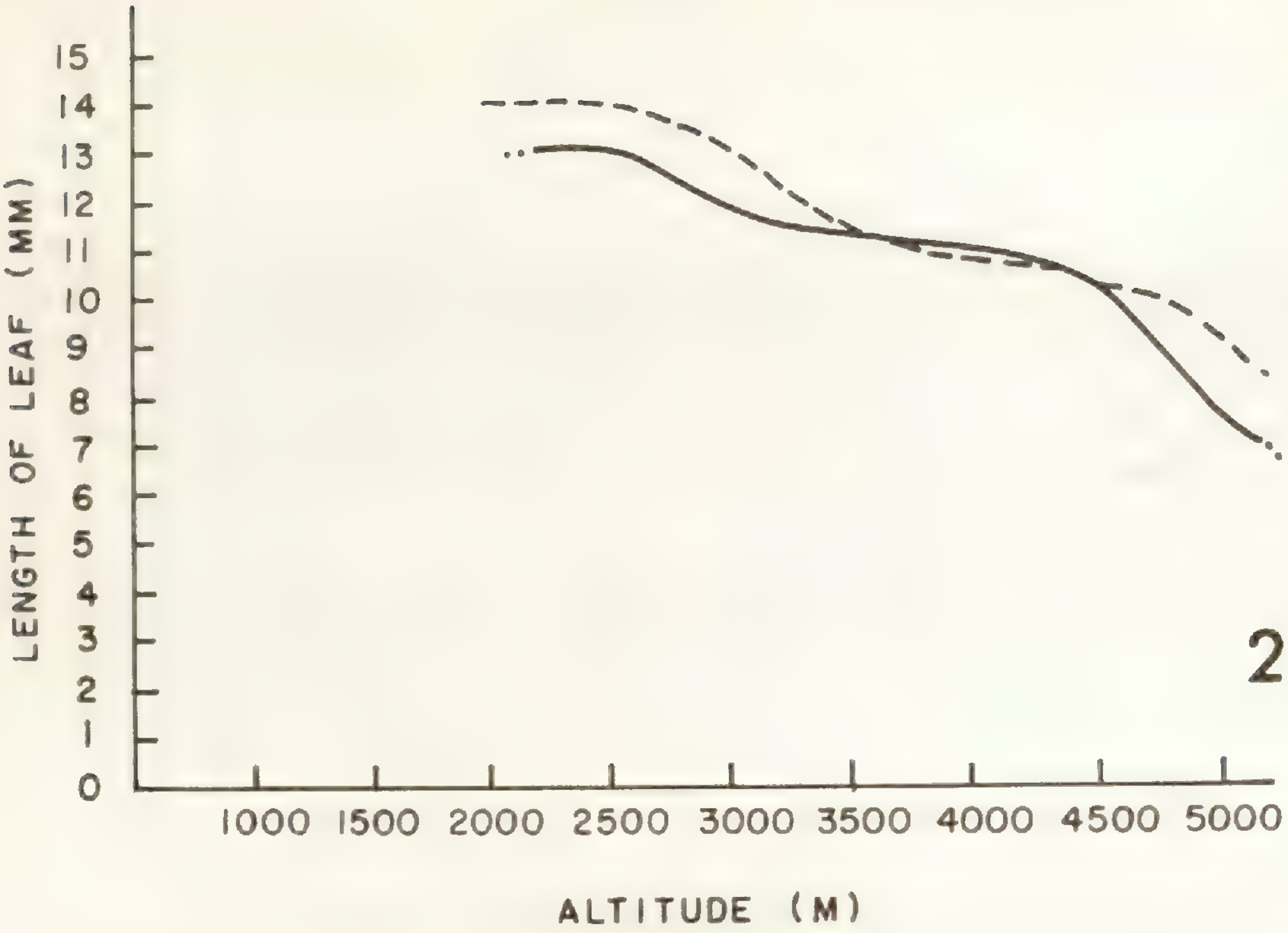
No noticeable modifications of shape are observed; this character, as well as the phyllotaxis, seems to be quite stable. Leaf length, on the other hand, varies in relation to elevation, both in America and in Africa and Madagascar (*Fig. 2*).

Similarly, plant height seems to diminish with elevation. *Figure 3* shows this in African populations. The lack of reliable data from American specimens makes a generalization impossible.

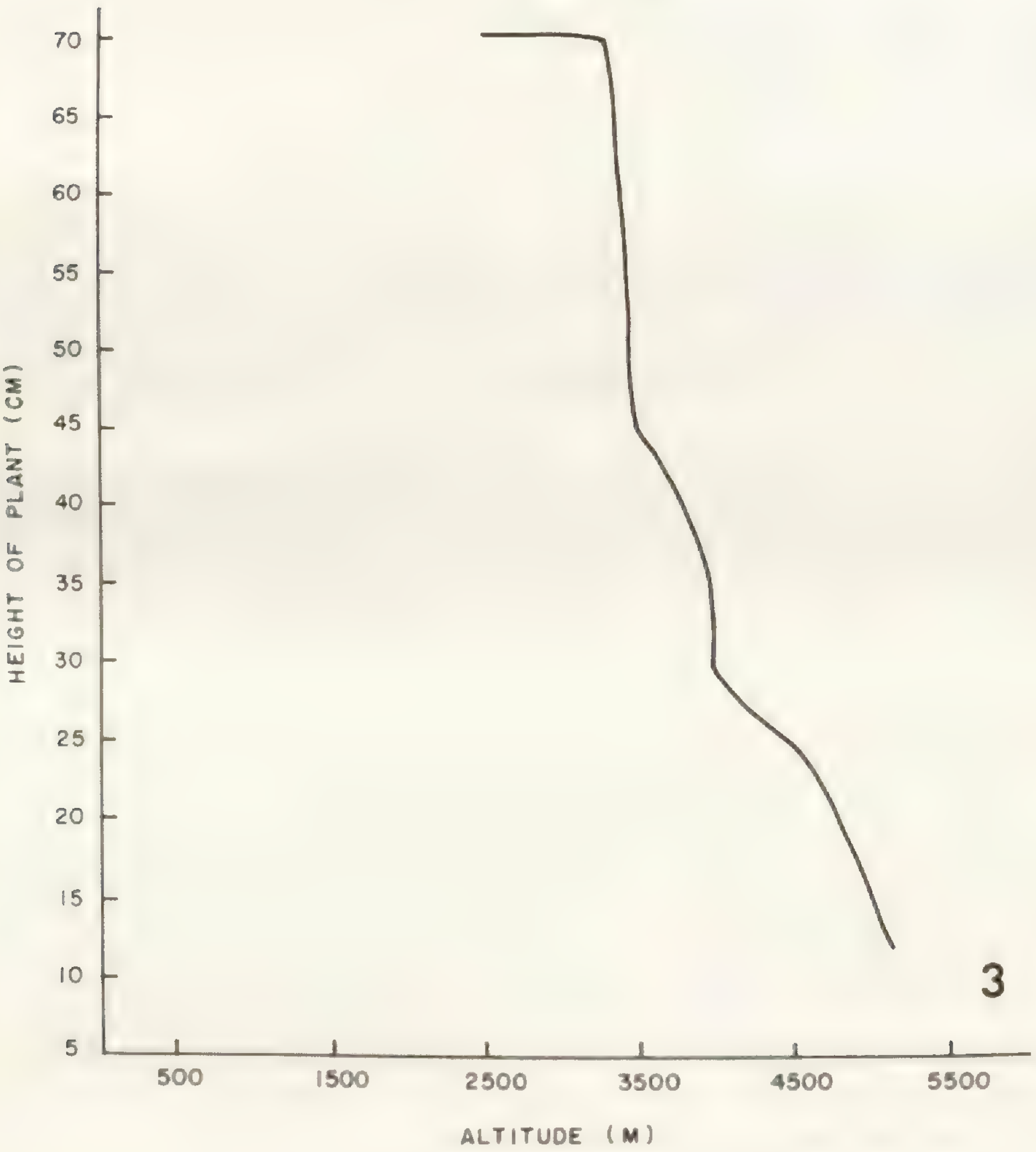
The most conspicuously variable characters of leaf anatomy lie in the typical, unmodified epidermal cells (shape, outline, wall thickenings, and modifications), in the stomata (shape, location, dimensions, and density), and in the modified epidermal cells which generally are on the marginal and apical portions of the leaves, although they can also cover the leaves.

The epidermis of *L. saururus* has a unique set of characteristics (Rolleri, 1972). It consists of a single layer of cells which vary in shape, but tend to be subrectangular, 2–3 times longer than wide, and have a sinuous outline. The middle lamella and the primary wall are evenly thickened (Rolleri, 1972) and form true sinuosities that are as broad as they are deep (*Fig. 4f*). Specialized epidermic cells always are restricted to the leaf margins.

The stomata of *L. saururus* are approximately orbicular to suborbicular. Their distribution is somewhat different on the two leaf faces: they are evenly distributed on the adaxial face (*Fig. 4b*), but are restricted to a submarginal band 3–5 stomata wide on the abaxial face (*Fig. 4a*). Stomatal density is given in *Table 2*; it varied a little in different geographical areas.


LENGTH OF LEAF (MM)
0
1
2
3
4
5
6
9
10
11
12
13
14
15
1000 1500 2000 2500 3000 3500 4000 4500 5000
ALTITUDE (M)

2


HEIGHT OF PLANT (CM)
5
10
15
20
25
30
35
40
45
50
55
60
65
70
500 1500 2500 3500 4500 5500
ALTITUDE (M)

3

The width of the stomatic band on the abaxial face is given in *Table 2*. The larger numbers are found at the leaf base. Stomatic dimensions (longer × shorter diameter) are also given in *Table 2*. In American specimens, the stomata are relatively narrower than they are in specimens from other areas.

The most remarkable character of the leaves of *L. saururus* is the peculiar morphology of the margins (*Fig. 5*). The mechanical marginal cells are quite different from the adjacent cells. They protrude, have very thick walls, are fusiform, tracheiform, or resemble blunt papillae, and project laterally or upwards. Their cell walls have large pits and sometimes are rugulose or have wrinkled surfaces. Several rows of these cells are clearly observable on both faces of the leaf.

TABLE 2. RELATIONSHIP OF STOMATAL DENSITY, ABAXIAL STOMATAL BAND WIDTH, AND STOMATE SIZE OF *Lycopodium saururus* THROUGHOUT ITS GEOGRAPHICAL RANGE.

Region	*Density on adaxial face*[1]	*Density on abaxial face*[1]	*Width of band*[2]	*Size on adaxial face*[3]	*Size on abaxial face*[3]
America	(7)13(15)	(5)7(9)	3–5(7)	(62)72(74) × (43)48(52)	(63)67(72) × (45)49(51)
Africa & Madagascar	(9)13(16)	(5)8(9)	2–5(7)	(65)72(74) × (48)54(58)	(62)67(72) × (48)55(58)
Réunion	(9)12(15)	(5)9(10)	3–5(8)	(64)68(70) × (50)53(56)	(62)66(70) × (50)54(56)

[1] Number per 0.25 mm² based on 25 counts on each of 25 leaves; extreme and mean values are given.
[2] Number of stomates across width of band based on 25 counts on each of 25 leaves; usual and extreme values given.
[3] Length and width in μm based on 25 stomates on each of 25 leaves; extreme and mean values given.

The combination of epidermal pattern and papillose margin identifies the leaves of *L. saururus* and clearly differentiates them from those of related species, which have a smooth and glossy epidermis. Both character states are stable, and no modifications have been observed with variations in elevation, latitude, or geographic area.

In sect. *Crassistachys*, epidermal modifications are frequent along the margin and rare on the surface. In certain cases, armored margins appear combined with superficial mechanical reinforcements composed of groups of fusiform cells located on the abaxial face. The cells of these groups are morphologically similar to the marginal ones and project above the general level of the epidermis. Such an epidermic modification of the abaxial face gives the texture and coriaceous consistency to *L. crassum* leaves.

The sporangium wall probably will prove to be an important character in the morphology and systematics of sect. *Crassistachys*. In *L. saururus* the most

FIG. 2. Relationship of altitude and leaf length in *Lycopodium saururus* from the Americas (broken line) and from Africa and Madagascar (solid line). FIG. 3. Relationship of altitude and plant height in *L. saururus* from Africa.

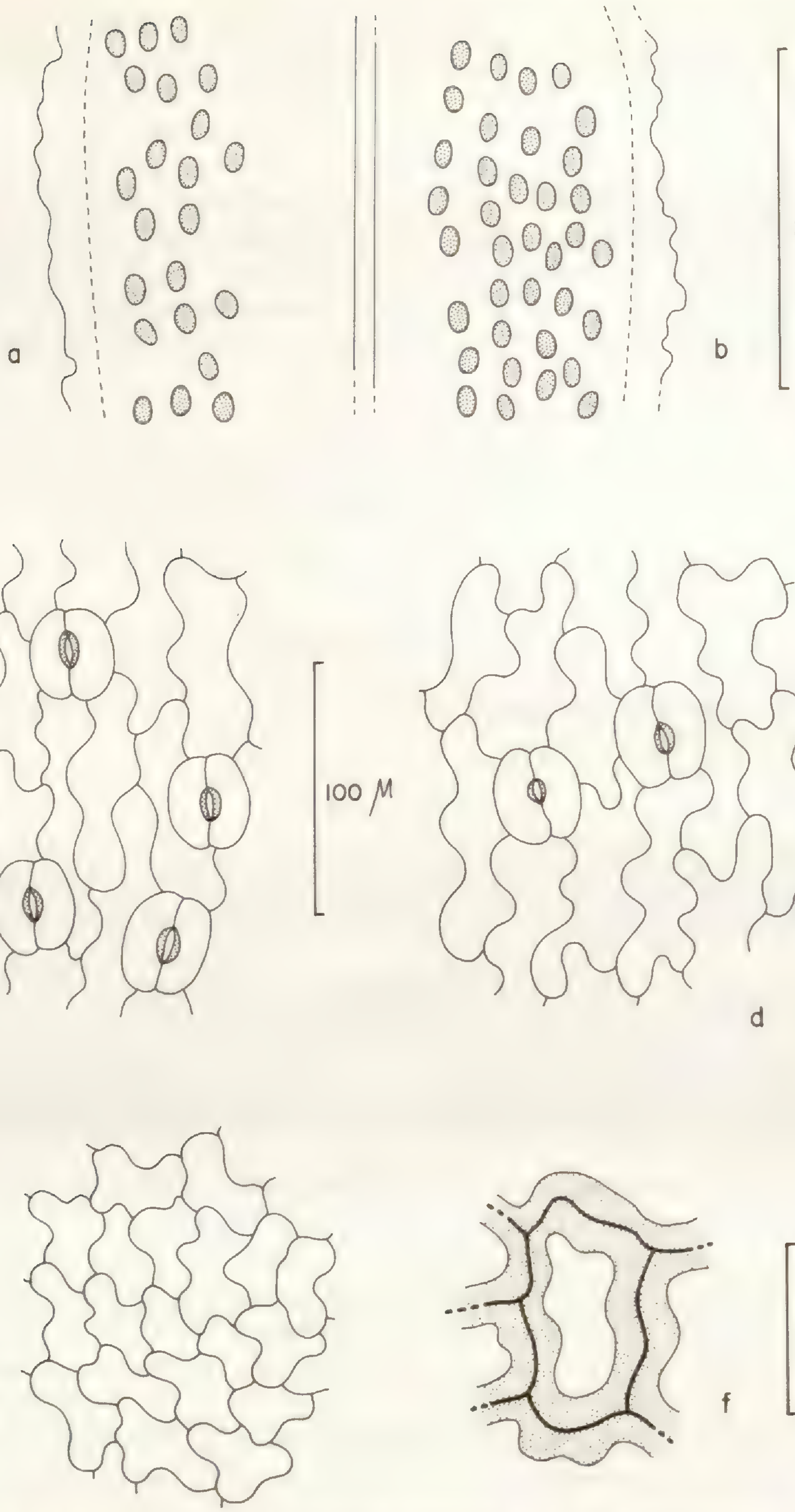


FIG. 4. Stomates and epidermal cells of *Lycopodium saururus*. FIG. 4a. Distribution of stomates on the abaxial leaf face. FIG. 4b. Same, adaxial leaf face. FIG. 4c. Abaxial epidermis. FIG. 4d. Adaxial epidermis. FIG. 4e. Sporangium epidermis. FIG. 4f. Detail of sporangium epidermal cell.

prominent traits of the sporangium wall are subrectangular cells 1–2 times longer than wide, with sinuous and remarkably thickened cell walls (thickenings 3–6 μm wide). The sinuosities are uniformly thick, shallow, and rather irregular (*Figs. 4e, f*).

Although the saxicolous species and some of the epiphytic ones share a similar sporangium wall morphology, a detailed analysis of the epiphytic species shows variations at the species level in cell outline and shape, sinuosities, and wall thickenings. In the specimens of *L. saururus* analyzed, no observable variation was found in the sporangium wall; the basic morphological characters of cell shape, outline (sinuosities), and wall thickening (width and uniformity) do not seem to be affected appreciably by the ecological variables.

CONCLUSIONS

Certain foliar characters of *L. saururus* are independent with respect to environmental variables. These include leaf shape, texture, phyllotaxis, stomate size, and epidermal and marginal cell structure.

Other characters, such as leaf length and, in certain cases, plant size, show variation that seems to correlate with elevation (*Figs. 2* and *3*). Plants growing at 4,000–5,000 m elevation have shorter leaves than those growing at lower elevations. The change in leaf length with respect to altitude is less in plants growing below 4,000 m elevation. Above that height, leaf length diminishes quickly with increasing elevation. Plant size is smaller with increasing elevation (*Fig. 3*). These conclusions coincide with those of Schelpe (1951) for plant communities for Mt. Kenya. He reported a marked diminution in *L. saururus*, from 60–70 cm for those growing in the upper level of the forest (2,500 m elev) to 10–12 cm for those living at the top "moorlands" (5,100 m elev). A similar situation seems to occur in American material of this species, but the scarcity of reliable data (many herbarium specimens have only fragments of branches) does not permit comparisons to be made.

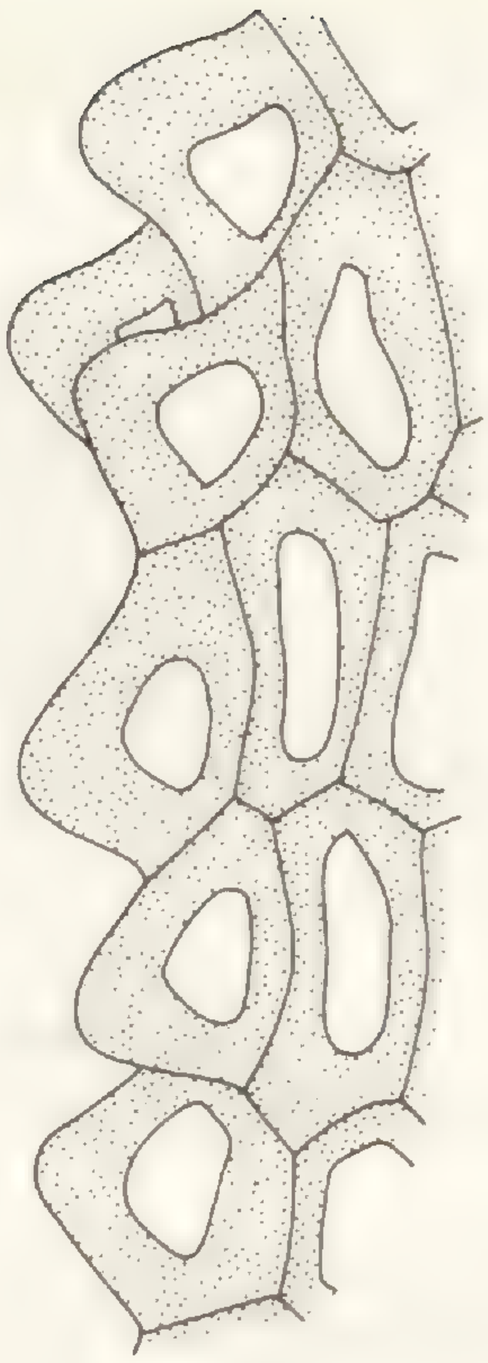
Soil is a factor that seems to be important. Together with elevation, it defines the ecological trends of this species and its affinity for mountainous environments, in continental as well as in insular environments. Schelpe (1951) mentioned the general diminution of plant size where the plants or the soil they have been growing on has been affected by fire.

Lycopodium saururus is typically a montane plant and has a wide range of elevational tolerance, as shown in the relative stability of the aforementioned characters betweeen elevations of 1,000 and 3,800 m.

This species has rather marked edaphic preferences with respect to nutrients, acidity, and regularity of soil moisture. Communities or specimens from loose and poor soils are reduced and dwarfed, and so are comparable to those growing at higher elevations.

Except for the aforementioned characters, the morphological variation of *L. saururus* is not very great, considering its wide distribution. Latitude does not alter the general proportions as elevation does, probably because the plants are

a



b

c

d

e

100 M

5 M

5

FIG. 5. Leaf margins in *Lycopodium saururus*. FIG. 5a. Near leaf apex. FIG. 5b. In median portion. FIG. 5c. Near leaf base. FIG. 5d. Detail of marginal cells in the apical and median portions. FIG. 5e. Detail of marginal cells near the leaf base.

confined to a single habitat which occurs as a geographical continuity, thus creating a migratory route of ample latitudinal range.

The variable morphological characters are not markedly modified with changes in environment or geographic area, and the morphological variation is statistically very low, considering the enormous distribution of this species. Given such variation, the strong disjunction, and the morphological correlations, the consideration of *L. saururus* as a species complex or the introduction of infraspecific categories is not justifiable. According to the preliminary morphological evidence, *L. saururus* is a homogeneous, relatively stable species with marked ecological preferences and a peculiar geographical distribution.

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Motozi Tagawa (1908–1977)

Dr. Motozi Tagawa was born in Osaka, Japan on April 11, 1908. During his high school years he developed an interest in fern taxonomy, and entered Kyoto University to learn plant taxonomy under Dr. G. Koidzumi. In the 1930's, when he started his botanical career, Japanese ferns were known quite insufficiently. He had to collect and identify the ferns even around Kyoto, and he described a number of new species that were based on specimens he collected in or near Kyoto. Naturally, his work was extended to include the ferns from every part of Japan, and he made a field trip to Yakushima Island in 1933 and to Taiwan three times between 1934 and 1940. Based on his own collections, as well as those sent to him from various parts of Japan, he developed greatly our knowledge of Japanese ferns. In 1959 he published a comprehensive "Coloured Illustrations of the Japanese Pteridophyta," which is a monumental work on the taxonomy of Japanese ferns and fern allies, although the text is in Japanese.

In 1965 Dr. Tagawa started to lead a project on the study of southeastern Asian flora. He made field trips to Thailand three times during 1965–1967 and published various papers on the ferns from Southeast Asia, making a great contribution to the flora of that area.

He took a part in the foundation of the Phytogeographical Society in 1932 and served as a member of the editorial board for "Acta Phytotaxonomica et Geobotanica" for about 45 years. The Japanese Pteridological Society was founded in 1957. It was proposed by Dr. H. Ito, the late Dr. S. Momose, and Dr. M. Tagawa, who served as its secretary for the first ten years. Dr. Tagawa belonged to the faculty of Kyoto University throughout his botanical life, and retired from the professorship of botany in 1972.

Dr. Tagawa died rather suddenly on July 19, 1977, of heart disease. By his death we will miss his knowledge of Asiatic pteridophytes very much. He prepared a great number of fine specimens which were distributed to various herbaria throughout the world. The life and work of Dr. Tagawa will be published in more detail in volume 29 of "Acta Phytotaxonomica et Geobotanica," along with a list of his main publications.—*K. Iwatsuki, Department of Botany, Faculty of Science, Kyoto University, Kyoto 606, Japan.*

SHORTER NOTE

OPHIOGLOSSUM CROTALOPHOROIDES NEW TO THE WEST INDIES.—Recent issues of this journal (**61:** 39- 41. 1971; **63:** 166. 1973; **64:** 119-120. 1974; **65:** 28. 1975) have included several discussions of range extensions for *Ophioglossum crotalophoroides* Walter within Louisiana and Mississippi and into Missouri and Georgia. Until now, however, the known range of this species has still been confined to the United States, Mexico, and Central and South America, as noted in Clausen's monograph (Mem. Torr. Bot. Club **19**(2): 1-177. 1938) and as cited, for example, in the recent and valuable first part of the Ferns of Guatemala by Stolze (Fieldiana, Bot. **39:** 1-130. 1976). The purpose of the present note is to report the considerable range extension of this species into the West Indies. Voucher collections were made by the author on August 20, 1967 *(Gastony et al. 725)* in the province of La Vega, Dominican Republic in a very moist timbered and burned-over pineland in the vicinity of the "pyramid" landmark about 13 km from Valle Nuevo on the road to San José de Ocoa. The plants were growing inconspicuously among grasses or fully exposed at the edge of an old sawdust pile and in an adjacent virtually unused dirt road at about 2500 m elevation. Specimens have been deposited at GH, NY, US, USD, and in the personal herbarium of the author.—*Gerald J. Gastony, Dept. of Biology, Indiana University, Bloomington, IN 47401.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of Drs. R. H. Eyde, R. M. Lloyd, J. H. Miller, A. R. Smith, R. G. Stolze, and J. J. Wurdack. We welcome suggestions of other reviewers and offers of assistance.—*D.B.L.*

REVIEW

"THE ORIGIN OF DRYOPTERIS CAMPYLOPTERA," by Mary Gibby. Canadian J. Bot. **55:** 1419-1428. 1977.—This admirable paper reports cytological analyses from various artificially synthesized hybrids. It continues a tradition of the work initiated by Manton and carried on by her students S. Walker, Lovis, Vida, etc., and now continuing into the next generation with Gibby doing doctoral research work with Walker. Artificial hybridization is an experimental tool which we pay homage to on this side of the Atlantic but unfortunately rarely emulate!

I would like to have known how many crosses were attempted, how many plants of each hybrid combination were obtained, and how many cytological plates were successfully analysed. However, I accept the facts that the hybrids were obtained and that the cytological results are representative of such hybrids.

One of the key crosses is *D. intermedia* (2*x*) × *D. assimilis* (2*x*) (diploid "*dilatata*") from Quebec. Gibby reports only 1–5 bivalents at meiosis in the hybrid, and consequently the stage is set to consider that the genomes of *D. intermedia* (II) are non-homologous with those of *D. assimilis* (AA). This should mean that *D. intermedia* is completely unrelated to *D. assimilis*, and the Europeans are then in a position to speak of the *D. intermedia* aggregate in contrast to the *D. assimilis* aggregate. This important step is difficult for us, because we have traditionally grouped *D. intermedia, D. spinulosa* (*carthusiana*), and *D. campyloptera* into the same confusing complex, at times just referring the whole to *D. austriaca*. Furthermore, Gibby's findings are a reversal of the position of Walker in 1961, who concluded that *D. intermedia, D. maderensis*, and *D. assimilis* have the same ancestral genomes.

The other seven crosses, the tetraploids *D. campyloptera* and *D. austriaca* from Europe crossed with various diploids, e.g., *D. assimilis, D. intermedia*, and *D. maderensis*, gave triploid progeny and meiotic analysis is interpreted as showing *n* bivalents (35–41) with ca. *n* univalents in each hybrid. From this, genome analysis suggests that *D. campyloptera* is indeed an allotetraploid with the constitution IIAA, i.e., the parents of *D. campyloptera* are *D. intermedia* and *D. assimilis* (the diploid "*dilatata*") in eastern North America).

The methods used have their limitations. The supposed reward for genome analysis is to identify safely an ancestral genome, e.g., II for *D. intermedia*, and thereby identify a biological species. *Dryopteris azorica* and *D. maderensis* have the same genomes as *D. intermedia*, but here are still considered to be separate species. Similarly, having interpreted *D. campyloptera* as an allotetraploid (IIAA) we are told that *D. austriaca* (4*x*) of Europe has the same origin (Gibby & Walker, 1977). Will we be able to maintain that *D. campyloptera* and *D. austriaca* are separate species?

To me, the most severe limitation of the method is relying on pairing behavior to identify either a classical alloploid or a classical autoploid. Both categories are probably idealized states or theoretical extremes. If we can extrapolate from recent work with wheat, it would seem that long-considered alloploids such as bread wheat are in fact segmental alloploids, and genes are now known which suppress chromosomal pairing as well as genes which enhance pairing. It now appears that chromosomes of *Triticum, Aegilops, Secale*, and perhaps even *Hordeum* have much in common, i.e., they are homoeologous. *Dryopteris campyloptera* does not fall neatly into either the autoploid or alloploid category. Chromatographic analysis suggested the former interpretation, and now cytological analysis suggests the latter. Perhaps by emphasizing similarities rather than differences, we can conclude that these species do have much in common—certainly many similar gene sequences and hence chromosomal homoeologies. Looked at this way, *D. campyloptera* would be a segmental allotetraploid and *D. intermedia* and *D. assimilis* would *not* be completely unrelated.

Keys, descriptions, and distributions to delineate the various taxa in this complex are still in the future.—*D. M. Britton, Department of Botany and Genetics, University of Guelph, Guelph, Ontario N1G 2W1, Canada.*

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